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Life History and Status of Shortnose Sturgeon (Acipenser brevirostrum LeSueur, 1818)

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Summary

Shortnose Sturgeon = SNS (Acipenser brevirostrum) is a small diadromous species with most populations living in large Atlantic coast rivers and estuaries of North America from New Brunswick, Canada, to GA, USA. There are no naturally land-locked populations, so all populations require access to fresh water and salt water to complete a natural life cycle. The species is amphidromous with use of fresh water and salt water (the estuary) varied across the species range, a pattern that may reflect whether freshwater or saltwater habitats provide optimal foraging and growth conditions. Migration is a dominant behaviour during life history, beginning when fish are hatchling free embryos (southern SNS) or larvae (northeastern and far northern SNS). Migration continues by juveniles and non-spawning adult life stages on an individual time schedule with fish moving between natal river and estuary to forage or seek refuge, and by spawning adults migrating to and from riverine spawning grounds. Coastal movements by adults throughout the range (but particularly in the Gulf of Maine = GOM and among southern rivers) suggest widespread foraging, refuge use, and widespread colonization of new rivers. Colonization may also be occurring in the

Potomac River, MD–VA−DC (mid-Atlantic region). Genetic studies (mtDNA and nDNA) identified distinct individual river populations of SNS, and recent range-wide nDNA studies identified five distinct evolutionary lineages of SNS in the USA: a northern metapopulation in GOM rivers; the Connecticut River; the Hudson River; a Delaware River−Chesapeake Bay metapopulation; and a large southern metapopulation (SC rivers to Altamaha River, GA). The Saint John River, NB, Canada, in the Bay of Fundy (north of the GOM), is the sixth distinct genetic lineage within SNS. Life history information from telemetry tracking supports the genetic information documenting extensive movement of adults among rivers within the three metapopulations. However, individual river populations with spawning adults are still the best basal unit for management and recovery planning. The focus on individual river populations should be complemented with attention to migratory processes and corridors that foster metapopulation level risks and benefits. The species may be extirpated at the center of the range, i.e., the mid-Atlantic region (Chesapeake Bay, MD–VA, and probably, NC), but large rivers in VA, including the James and Potomac rivers, need study. The largest SNS populations in GOM and northeastern rivers, like the Kennebec, Hudson, and Delaware rivers, typically have tens of thousands of adults. This contrasts with southern rivers, where rivers typically have much fewer (<2,500) adults, except for the Altamaha River (>6,000 adults). River damming in the 19th and 20th Centuries extirpated some populations, and also, created two dysfunctional segmented populations: the Connecticut River SNS in CT−MA and the Santee-Cooper rivers−Lake Marion SNS in SC. The major anthropogenic impact on SNS in marine waters is fisheries bycatch. The major impacts that determine annual recruitment success occur in freshwater firstly, where adult spawning migrations and spawning are blocked or spawning success is affected by river regulation and secondly, where poor survival of early life stages is caused by river dredging, pollution, and unregulated impingement-entrainment in water withdrawal facilities. Climate warming has the potential to reduce abundance or eliminate SNS in many rivers, particularly in the South. In 1998, the National Marine Fisheries Service (NMFS) recommended management of 19 rivers as distinct population segments (DPSs) based on strong fidelity to natal rivers. A Biological Assessment completed in 2010 reaffirmed this approach. NMFS has not formally listed DPSs under the ESA and the species remains listed as endangered range-wide in the USA.

Introduction

It has been 32 yr since the review of Shortnose Sturgeon = SNS (Acipenser brevirostrum) by Dadswell et al. (1984) and 19 yr after the species review by Kynard (1997). Since the 1997 review, life-history research on rivers in ME and southern rivers found greater movement of SNS among river-estuary systems than previously known, added new information on abundance and status in

several rivers, and identified some rivers as places where foraging-refuge seeking occurs, but spawning does not occur. Further, new information on population structure and inter-river genetic exchange is now available from range-wide genetic analysis. Additionally, new information was discovered on many aspects of SNS life history (spawning behaviour, early life history, foraging and wintering habitat selection), impact of damming and river regulation on migrations and spawning), and research began to address methods for upstream and downstream passage at dams. Some of the new information was included in the latest status review for NMFS (Shortnose Sturgeon Status Review Team, 2010). Much of the new information is on a long-term study of Connecticut River = CR SNS and is included in the present review.

In the present review, the expertise of scientists studying SNS in the field and laboratory throughout the range has been utilized. Managers from NMFS also contributed the latest information on recovery efforts and research needs for management. We hope this review will provide hypotheses to test and guidance to SNS researchers and managers for many years.

Taxonomy and Phylogeny

Acipenser brevirostrum LeSueur, 1818: 390

Synonyms

Acipenser brevirostris Richardson, 1836: 278; Acipenser (Huso) microrhynchus Duméril, 1870: 164; Acipenser (Huso) lesueurii Duméril (ex Valenciennes), 1870: 166; Acipenser (Huso) dekayii Duméril, 1870: 168; Acipenser (Huso) rostellum Duméril 1870: 173; Acipenser (Huso) simus Duméril (ex Valenciennes), 1870: 175.

American Fisheries Society English common name. Shortnose Sturgeon
Quebec French vernacular name. Esturgeon à nez court
Other vernacular names. round-nosed sturgeon, shortnosed sturgeon, pinkster, roundnoser, bottle-

nose, mammose, salmon sturgeon, soft-shell sturgeon, and lake sturgeon (Dadswell et al., 1984).

Phylogeny

SNS traditionally has been considered closely related to Lake Sturgeon = LS (A. fulvescens) based on overall similarity in aspects of their morphology (e.g., mouth width, number of gill rakers, black viscera; Vladykov and Greeley, 1963), and this was the conclusion of Artyukhin (1995). In their review and synthesis of Artyukhin's data and interpretations, Choudhury and Dick (1998) also concluded that SNS and LS were sister-taxa based on a single synapomorphy (presence of dark blotches of pigment on the body in juveniles). Artyukhin (2006) analyzed the distribution of 28 morphological characters across Scaphirhynchus, Pseudoscaphirhynchus, and all species of Huso and Acipenser. In this analysis, he found SNS to be in a group that also included Persian Sturgeon (A. persicus), Russian Sturgeon (A. gueldenstaedti), Adriatic Sturgeon (A. naccarii), and LS. This group was defined by the presence of short dorsal rostral bones and the barbels positioned close to the tip of the snout. Within this group, SNS was considered to be the sister-group of LS + Siberian Sturgeon (A. baeri), which was based on characters related to body color. While it is unclear which characters supported this position of SNS, Artyukhin (2006) noted that "In cultured inbred groups of Siberian Sturgeon, rare juveniles demonstrate dark spots and blotches on the body," and that this character was typical in LS, SNS, and Adriatic Sturgeon. In a cluster analysis of morphological data (cranial measurements and gill raker shape), Vasil'eva (2004) found similarity between SNS and Adriatic Sturgeon, Russian Sturgeon, and Persian Sturgeon, and noted that a similar clade has been discovered in recent molecular analyses (see below). In a recent morphological phylogenetic analysis building from their descriptive osteology of SNS, Hilton et al. (2011; see also Hilton and Forey, 2009) found SNS and LS to be sister-taxa based on the presence of a uniquely shaped jugal bone (triangular in lateral view rather than shaped like a reversed L, as in other sturgeons).

Although the number of characters was significantly greater compared to that of Artyukhin (62 versus 28 characters, respectively), only seven species of Acipenser were included in this analysis and the usefulness of this character must be tested by inclusion of all species of Acipenser.

In contrast to the results of morphological studies, using partial sequences of cytochrome b, 12S rRNA, and 16S rRNA for the analysis of relationships among Scaphirhynchus, Huso, and all species of Acipenser, Birstein and DeSalle (1998) found SNS to be the sister species of Russian Sturgeon, which was in turn sister to the group (Adriatic Sturgeon, Siberian Sturgeon, Persian Sturgeon, Stellate Sturgeon, Ship Sturgeon (A. nudiventris), and Dabry's Sturgeon (A. dabryanus); therefore, SNS was found to be only distantly related to LS. Birstein et al. (2002), using sequences from additional mitochondrial loci and expanded taxon sampling (e.g., including Pseudoscaphirhynchus), found SNS to be the sister-species of a clade including Siberian Sturgeon, Russian Sturgeon, Adriatic Sturgeon and Persian Sturgeon (this result is consistent with that of Zhang et al. (2000), although the study of Zhang et al. only included Adriatic Sturgeon among these taxa). In Birstein et al.'s (2002) analysis, the position of LS relative to this grouping, however, was unresolved. In a combined analysis including their genetic data and morphological data adapted from Mayden and Kuhajda (1996), Birstein et al. (2002) found LS again to be relatively far from the group including SNS, albeit with reduced taxon sampling.

In the studies of Ludwig et al. (2000) and Fontana et al. (2001), using sequences from the entire cytochrome b gene, SNS was found to be the sister-species of the clade including Siberian Sturgeon, Russian Sturgeon, Adriatic Sturgeon and Persian Sturgeon (although the relationships among these taxa varied between the two studies); LS was found to be the sister-species to this clade in both studies (i.e., relatively more closely related to the clade including SNS than found in the analysis of Birstein et al. (2002). Statistical support for this position of LS was relatively strong

(quartet-puzzling value of 99% in Ludwig et al., (2000), and 99% bootstrap in Fontana et al. (2001). In a maximum parsimony analysis of sequences from the control region and cytochrome b for 12 species of Acipenser, beluga (Huso huso), and all extant species of Pseudoscaphirhynchus and Scaphirhynchus, Dillman et al. (2007) found that SNS formed an unresolved polytomy with LS, Beluga, the clade (Siberian Sturgeon, Russian Sturgeon [gueldenstaedti subspecies], Persian Sturgeon, Adriatic Sturgeon, and Russian Sturgeon [colchicus subspecies], and the clade Stellate Sturgeon + Pseudoscaphirhynchus. However, using the same sequence data in a Bayesian analysis, Dillman et al. (2007) found LS and SNS to be sequential sister-groups of the clade including Huso, Siberian Sturgeon, Russian Sturgeon, Persian Sturgeon and Adriatic Sturgeon; these nodes were supported by high posterior probabilities (99 and 94, respectively). In a recent maximum likelihood analysis of sequences from eight mitochondrial genes for all species of Scaphirhynchus, Huso, Acipenser, and P. kaufmanni, Krieger et al. (2000, 2008) obtained results similar to that of Ludwig et al. (2000), Fontana et al. (2001), and Dillman et al. (2007), with LS sister to the clade SNS (A. baerii (A. gueldenstaedtii (A. persicus, A. naccarii); all nodes of this clade were very strongly supported (quartet puzzling values >99%) except A. persicus + A. naccarii (89%). This result was different from that of the earlier study by Kreiger et al. (2000) based on mitochondrial data, in which SNS and LS were recovered as sister-species, a result that was likely an artifact of taxon sampling (i.e., only North American species of sturgeons were investigated).

Geographic Distribution and Abundance

All evidence suggests that historically, all large rivers on the Atlantic Coast of the United States had natal SNS populations that coexisted with Atlantic Sturgeon = AS (A. oxyrinchus oxyrinchus; Dadswell et al., 1984). This is a classic example of a sturgeon species pair (large and a small sturgeon species) inhabiting the same river (Bemis and Kynard, 1997). Because all sturgeons along

the Atlantic coast were called “common sturgeon” in the commercial catch statistics (Murawski and Pacheco, 1977), it is impossible to estimate historic abundance and distribution of SNS as capture records combined AS and SNS until SNS was listed under the Endangered Species Act (USDI, 1973).

The distribution of SNS is summarized in the following account. Known spawning populations (from North to South) occur from the Saint John River = SJohnR, Bay of Fundy, NB, Canada, to the Altamaha River = AltR, GA, USA (Fig. 1). Within this range, some rivers have spawning populations, while others only have non-spawning adults (and studies continue to reveal whether spawning occurs in some rivers; Fig. 1). In the USA, from North to South, SNS occur in the Gulf of Maine = GOM -- Penobscot River = PenobR, Kennebec River = KenR, Androscoggin River = AndR, and the Merrimack River = MR. Farther south, there are three northeastern rivers, each with a spawning population: the Connecticut River = CR, Hudson River = HudR, and Delaware River = DelR. Shortnose Sturgeon occur in the Chesapeake Bay and in the Potomac River = PotR (discussed in the mid-Atlantic Section along with VA rivers). Spawning SNS populations seem absent in NC rivers. Southern rivers with SNS (but not necessarily independent spawning river populations; Fig. 1) are the Great Pee Dee River = GPeeDR, Cooper River = CoopR, Santee River = SantR, Congaree River = CongR, Edisto River = EdisR, Savannah River = SavR, Ogeechee River = OgeeR, and the Altamaha River = AltR. Additional populations in SC may occur in Winyah Bay rivers (in addition to the GPeeDR) and in other rivers in the ACE basin (Ashepoo and Combahee Rivers, in addition to the EdisR).

The following section reviews information from rivers within each geographic region (Bay of Fundy-GOM, northeastern, mid-Atlantic, and southern) for SNS early life stages = ELS (egg, free embryo, and larva) that have been observed, the presence of young juveniles (YOY to yr-3),

183 and population abundance. Rivers where the status of SNS is unclear are discussed in detail.

184

185 **A. Bay of Fundy and GOM rivers**

186 In the SJohnR, Bay of Fundy (Fig. 1), ELS and young juveniles have been captured showing
187 spawning and recruitment occur (COSEWIC, 2005; Usvyatsov et al., 2012a; Fig. 2). Estimated
188 abundance of adults in the SJohnR estuary was 18,000 during the 1970s (Fig. 3; Dadswell et al.,
189 1984). Recent efforts to estimate adult abundance in a SJohnR tributary (Kennebecasis R.) using
190 underwater observations on overwintering adults (Usvyatsov et al., 2012b) found abundance was
191 3852 and 5222. These estimates agreed well with a local population estimate of 4836 adults.
192 However, no recent estimate of total abundance of adult SNS in all wintering reaches of the
193 SJohnR is available.

194 Gulf of Maine rivers with SNS spawning follow: 1) the AndR (Squiers et al, 1993), 2) the
195 KenR (Wippelhauser, 2003), and 3) the MR (Kieffer and Kynard, 1996; Fig. 1). Additionally, in
196 the MR, young juveniles have been captured (Fig. 2), providing evidence for possible recruitment.
197 GOM population estimates (Fig. 3) are old (Kynard, 1997). The MR has the smallest spawning
198 population of SNS known with only tens of adults present (Kieffer and Kynard, 1996). Shortnose
199 Sturgeon in the MR are freshwater amphidromous, like all populations of northeastern SNS with
200 juveniles and adults mostly using fresh water, while SNS in Bay of Fundy or GOM rivers use
201 saltwater for foraging as juveniles and adult.

202 Although estimates suggest 600–1500 adults, including late-stage females, use the PenobR,
203 for foraging and wintering refuge, no spawning has been documented or ELS captured in more
204 than 4 yr of sampling (Fernandez, 2008, et al., 2010; Dionne, 2010; Kinnison, M., unpbl. data.).
205 Thus, as indicated on Fig. 1, a spawning population in the PenobR is unlikely and SNS are part of

206 the GOM metapopulation that spawn in the KenR and forage and overwinter in the PenobR
207 (Wippelhauser et al., 2015). It will be interesting to learn if SNS colonize and spawn in the PenobR
208 after the lowermost dams are removed.

209 Recent tracking of adult SNS in the GOM found some fish used the lower reaches of small
210 non-natal coastal rivers for short visits, probably to forage (Zydlewski et al., 2011). Further,
211 tracking of telemetry-tagged adults from three GOM rivers found movement between rivers (Little
212 et al., 2013) and a one-step or two-step spawning movement (Bemis and Kynard, 1997) into the
213 KenR, where removal of Edwards Dam has created presumed spawning habitat (Wippelhauser et
214 al., 2015). Inter-basin movements may be typical of metapopulation SNS (northern or southern)
215 that have a large home range including estuaries and rivers far from their natal river. The coastal
216 movements by adult SNS may be a critical part of life history that provides the opportunity to
217 colonize rivers.
218
219 **B. Northeastern rivers**
220 Spawning populations occur in each of the three northeastern rivers (Fig. 1). In these rivers, SNS
221 have a strong freshwater amphidromous life history: the CR (Taubert, 1980a; Taubert and
222 Dadswell, 1980; Kynard et al., 1999, 2000, 2012a, b; Kieffer and Kynard, 2012a, b, c); the HudR
223 (Bath and O'Conner, 1981; Hoff et al., 1988; Dovel et al., 1992; Bain, 1997), and the DelR
224 (O'Herron et al., 1993; Environ. Res. and Consult., Inc., 2008). In these rivers, ELS and young
225 juveniles occur (Fig. 2) indicating a spawning population exists with recruitment to the adult life
226 stage.

227 Beginning in the 1970s, CR SNS upstream of Holyoke Dam was called a land-locked
228 population (Taubert, 1980a, b; Dadswell et al., 1984) and questions about the status of the group of

229 SNS upstream of the dam remain for some biologists (Savoy, 2004). However, all scientific
230 evidence indicates characterization of the upstream group as land-locked is an error—they are
231 dam-locked. Extensive studies on life history movements of SNS upstream and downstream of the
232 dam (Kynard et al. 1999, 2012a, b, d, e) and genetic comparison of the upstream and downstream
233 groups (Wirgin et al., 2005) agree-- there is one population that was divided into a dam-locked
234 upstream segment and a downstream segment when Holyoke Dam was completed in 1849.
235 Spawning in this segmented population has been studied (Kynard et al., 2012a, b; Kieffer
236 and Kynard, 2012a; Fig. 2) and because the population segments are unable to complete natural
237 migrations and spawning, the result is a smaller population compared to other northeastern rivers
238 (Fig. 3). Abundance of adults in the downstream segment was estimated by mark-recapture in CT
239 from 1988−2002 as 1100−1600 adults (Savoy, 2004). Abundance increased with year of sampling
240 with the greatest abundance in the 1996−2002 period (Savoy, 2004), indicating a slight trend for
241 increased abundance. Further, the estimate for 2001 and 2002 was 1667 and 1874 adults,
242 respectively, which would include recruits spawned in 1995, the peak spawning year during 17 yr
243 of observation at the upstream segment's spawning site (Kieffer and Kynard, 2012a). Abundance
244 in the upstream segment was estimated using mark-recapture in the 1900s at 328 adults (Kynard et
245 al., 2012a; Kieffer and Kynard, 2012a). If these estimates have not changed with time, there would
246 be about 2000 adults in the present segmented population, but only 300 or so adults in the effective
247 breeding population = the upstream segment (Kynard et al., 2012a). Only a few hundred adults
248 produce all the recruits for both segments of the population, because each year about 50% of the
249 yearling juveniles produced by the upstream segment migrate downstream to the lower river
250 (Kynard et al., 2012d).

A range-wide analysis of SNS abundance found adult abundance had a significant and positive relationship with upstream spawning distance, i.e., the distance from river mouth to the spawning reach (Kynard, 1997). This analysis indicated there should be 28,000, not 2000, CR adults. Abundance of SNS in northeastern rivers is typically tens of thousands of adults, except for the segmented CR population (Kynard et al., 2012a; Fig. 3). Damming and segmentation of the CR population in the mid-19th Century continues to have a great deleterious impact on adult abundance, survival, and growth (Kynard et al., 2012a).

The HudR has the greatest abundance of any SNS population, estimated in the 1990s at about 38,000 adults (Bain, 1997; Fig. 3). Spawning and production of ELS has been verified in the river (Hoff et al., 1988; Dovel et al., 1992) and production of young juveniles has been strong during the past 40 yr (Fig. 2; Bain, 1997). Thus, present abundance of adults may be more than the 38,000 adults estimated by Bain.

Among the three northeastern rivers, the DelR has the longest un-dammed mainstem reach (Kynard, 1997) and it is the only river to have the spawning site unassociated with or unaffected by the lowermost mainstem dam. Juvenile production has been verified (Fig. 2; Brundage and O'Herron, 2009). The DelR is joined to the Chesapeake Bay via the Chesapeake and Delaware Canal through which DelR SNS migrate into Chesapeake Bay (Welsh et al., 2002). Abundance of DelR SNS was estimated at 13,000 adults in the 1990s (O'Herron et al., 1993; Fig. 3).

Surveys for SNS in another northeastern river, the Taunton River, MA (not on Fig. 1) discovered foraging juvenile AS, but no SNS (Burkette and Kynard, 1993). No other river in the northeastern region seems to have a SNS population.

C. Mid-Atlantic rivers

Although SNS adults occur in Chesapeake Bay (Welsh et al., 2002), there is little evidence for

spawning SNS populations in any river within the bay. Small numbers of adults (<10) have been observed in the lower Susquehanna River, PA-MD (not on Fig. 1) downstream of Conowingo Dam (lowermost dam on the river only 10 rkm upstream from the estuary; Mangold, M., Annapolis Field Station, USFWS, Annapolis, MD, unpbl. data). Welsh et al. (2002) found emigration of DelR adults into Chesapeake Bay and reverse movement; and further, Grunwald et al. (2002) found no genetic difference between DelR adults and adults captured in Chesapeake Bay. Thus, all evidence indicates the DelR is providing foraging and colonizing adults to Chesapeake Bay and its rivers.

The only river in the mid-Atlantic (including Chesapeake Bay) where there is evidence of either a remnant SNS population or an ongoing colonization from the DelR is the PotR (Fig. 1). An adult SNS specimen in the National Museum of Natural History (Smithsonian Institution; USNM 16730, collected on 19 March 1876 by J. Milner in the PotR at Washington, DC (the same month a mature telemetry-tagged female migrated to spawn in DC; Kynard et al., 2009) suggests a natal population existed in the PotR and likely spawned in the same river reach at DC. However, no early life stages or young SNS have been observed in the PotR. South of the PotR in VA is the James River (not on Fig. 1), where spawning adult and juvenile AS are present (Balazik et al., 2012), and also, the Rappahanock and York rivers (not on Fig. 1), where juvenile AS occur. Shortnose Sturgeon may also be present in these rivers, but no direct evidence (i.e., a specimen) is available despite a USFWS anadromous fish restoration program in VA.

Sampling for sturgeons in the Neuse River, NC (not on Fig. 1), located north of the CapFR (Fig. 1) captured 10 juvenile AS, but zero SNS (Oakley and Hightower, 2007). Except for the occasional coastal migrant, SNS seem absent from NC rivers (but see CapFR in the Southern rivers Section).

In summary, commercial fishing records indicate most or all mid-Atlantic rivers historically

297 had sturgeon populations. However, despite sampling targeted for sturgeons in recent decades,
298 there has been no documented spawning and few or zero SNS captured or observed in any mid-
299 Atlantic river.
300
301 **D. Southern rivers**
302 In the 1990s, adult SNS males and females were captured in the CapFR located in southern NC
303 (Fig. 1). These pre-spawning adults were tracked migrating upstream to spawn before being
304 blocked by the lowermost USACE dam (Moser and Ross, 1995). This migration strongly suggests
305 a SNS population occurred in the CapFR, but was slowly being extirpated by the inability to pass
306 the dam and spawn upstream. Successful spawning downstream of the dam was unlikely due to
307 presence of only sandy substrate, but spawning success was not studied downstream of the dam.
308 Whether the CapFR still has SNS is not known. No SNS were captured in any NC river to include
309 in the range-wide genetic analysis of King et al. (2014; see Genetics Section) and only coastal
310 migrant SNS from other rivers may presently occur in NC waters.
311 Capture of ELS or young juveniles (Fig. 2) has been documented in six southern rivers. Four
312 rivers are in SC: the GPeeDR (Collins, M., unpbl. data), CoopR (Cooke and Leach, 2004)**,** CongR
313 (Collins et al., 2003), and the EdisR (Smith et al., 2002). The fifth river, the SavR (Collins et al.,
314 2002) borders SC and GA, and the sixth river is the AltR in GA (Devries & Peterson, 2006; Fig 1).
315 The GPeeDR is part of the Winyah Bay river−estuary system. This system supported the
316 largest historical sturgeon fishery in the South (NMFS, 2007). For Winyah Bay rivers, the presence
317 of young juveniles indicates SNS may spawn only in the GPeeDR (Collins, M., unpbl. data; Fig.
318 2). Spawning in other rivers within this system may occur, but more study is needed.
319 Within the altered Santee-Cooper river drainage, SNS spawning occurs at two places: 1) in

320 the CoopR in the highly altered tailrace downstream of Pinopolis Dam, and 2) at a natural reach in
321 the CongR, which joins the upper-SantR upstream of the all dams (Fig. 1). The Santee-Cooper
322 basin system is a complex of rivers, tributaries, dams, canals, and impoundments created by the
323 USACE to divert the major river flow from the SantR to Pinopolis Dam (on the CoopR) for
324 hydroelectric generation. The CoopR was formerly a short, low gradient coastal river whose
325 headwaters never reached the fall line, where stream slope increases and a rocky bottom appears
326 creating SNS spawning habitat (Collins et al., 2003). Thus, the historical CoopR was an unlikely
327 site for SNS spawning. The SantR (including the CongR), probably contains the upstream segment
328 of the historic population that was divided by damming and diversions, and which presently
329 spawns successfully in the CongR (Figs. 1, 2). Adults currently inhabit upstream and downstream
330 reaches of the two lowermost impoundments (lakes Marion and Moultrie), including the
331 impoundments (Collins et al., 2003). In summary, damming in the SantR basin in the 1940s
332 divided the SNS population into a dam-locked group upstream of the dams and reservoirs that
333 continues to spawn and produce young sturgeon in the CongR, and a coastal segment below the
334 dams, whose upstream spawning migration is blocked by the dams.
335 Although adult SNS spawn in the CoopR at the power station tailrace at Pinopolis Dam
336 (Duncan et al., 2004), when telemetered pre-spawning adults at Pinopolis Dam were displaced
337 upstream of the dam, they continued upstream migration through the reservoir system to the
338 CongR (Finney et al., 2006). This movement suggests adults were homing to the river reach where
339 they were spawned. Juveniles and adults spawned in the CongR that leave the CongR and move
340 downstream past the reservoir and dam system are believed to maintain SNS in the lower SanR,
341 CoopR, and estuary. Although pre-spawning adults migrate upstream in the CoopR and spawn
342 downstream of Pinopolis Dam, the few juveniles in the CoopR casts doubt on whether this

343 reproduction successfully produces recruits (Wirgin et al., 2009). All evidence suggests adults in
344 the CoopR were likely spawned upstream in the CongR and migrated downstream during life
345 history, like upstream segment CR SNS, or they are coastal migrants from other rivers (Wirgin et
346 al., 2009). Further, if the dispersal of free embryos and larvae spawned in the CoopR is like the
347 dispersal found for nearby SavR SNS ELS (Parker and Kynard, 2005; Parker, 2007; Parker and
348 Kynard, 2014), they have a long dispersal and will die when they reach salt water < 20 km
349 downstream from Pinopolis Dam. Like all sturgeons, SNS free embryos and larvae lack tolerance
350 to salinity (Jenkins et al., 1993). Adult abundance in the SanR-CoopR is estimated in the 100s (Fig.
351 3). More study is needed to identify the natal river of these spawning adults and to provide fish
352 passage at the dams.

353 Although there are no historical records of SNS in the EdisR, a river in the ACE Basin (Fig.
354 1), recent captures of young juveniles indicates successful spawning and recruitment occurs
355 (Collins, M., unpbl. data; Fig. 2). However, no abundance estimate for EdisR SNS is available
356 (Fig. 3). A complicating factor for estimating abundance of SNS in the EdisR is that it may contain
357 SNS emigrants from the group of almost 100,000 cultured SavR juveniles (most unmarked) that
358 were released into the SavR during 1985−1992 (Smith et al., 2002). Recapture of some marked
359 SavR juveniles in rivers throughout the southeast coast show these unmarked fish have entered
360 many rivers, possibly including the EdisR.

361 Spawning has not been documented by collection of ELS in the SavR, but yr-1 juveniles
362 occur at the saltwater: freshwater interface in the lower river (Hall et al., 1991; Collins et al., 2002;
363 Fig. 2). Many of these juveniles overwinter at or just upriver of the Kings Island Turning Basin,
364 suggesting spawning and survival to yr-1 in the SavR is successful (Fig. 2). Adult abundance is
365 estimated in the 1000s (Fig. 3); however, this estimate is greatly influenced by the thousands of

366 unmarked cultured juveniles stocked during the 1980s and 1990s (Smith et al., 2002). The long-
367 term effects of this stocking are unknown. Similar stockings have not been repeated in any other
368 river and the widespread coastal movements of SNS throughout the range make conservation
369 stocking a poor management choice.

370 Years of study on SNS in the OgeeR found adult abundance was estimated at 100s (Fig. 3).
371 However, spawning or the presence of ELS or young juveniles has never been documented
372 (Rogers and Weber, 1994a, b; Fig. 2). Further, the lower river has a degraded environment (Jager
373 et al., 2013). The OgeeR is apparently only used by non-natal adults to forage or seek refuge in
374 summer (Peterson and Farrae, 2011).

375 The AltR is the longest river on the southeastern Atlantic Coast. This long undammed river
376 supports the largest southern population of SNS, which was recently estimated at >6000 adults
377 (Devries and Peterson, 2006; Fig. 3). Presence of yearlings and older juveniles has been confirmed
378 (Fig. 2) and a great level of annual variability documented for juvenile abundance (Peterson and
379 Bednarski, 2013). Spawning reaches have been identified (Devries and Peterson, 2006) but no
380 detailed studies on spawning have been done.

381 Since the Recovery Team identified 19 rivers with SNS populations (NMFS, 1998), the
382 status of SNS in southern rivers has changed. Only a few infrequent captures of single adult SNS
383 has occurred in the three most southerly rivers once thought to have populations (St. Marys and
384 Satilla rivers, GA; St. John's River, FL; not on Fig. 1). There is no evidence of spawning in any of
385 these rivers (Rogers and Weber, 1994a, b; Peterson, D., unpbl. data; Cooke, D., S.C. Dep. Nat.
386 Resour., Bonneau, unpbl. data). These rivers may always have only been used for foraging and
387 refuge by non-natal adults. As expected for coastal migrants, a few adult SNS continue to be
388 captured in the St. John's River (one adult originally tagged in the Satilla River captured in 2000)

and another untagged adult (source unknown) captured in 2002 (Fl. Wildl. Comm., press release). In summary, recent evidence shows the AltR is the southernmost river with a SNS population and that several rivers, previously believed to have populations, are only used for foraging, refuge, or both (Cooke and Leach, 2003; Peterson and Farrae, 2011).

E. Concentration reaches

Within their natal river-estuary range, SNS are not distributed randomly, but instead home to certain reaches to forage and seek refuge. These reaches were first termed concentration areas by Buckley and Kynard (1985a). These areas or reaches may be in fresh water or in the estuary. In the CR, the only population where concentration use has been intensively studied, homing fidelity and use of the reaches was on an individual life history schedule depending on their reproductive schedule (Kynard, 1997; Kynard et al., 2012a, e). This behaviour may be genetic because the seasonal use of concentration reaches and habitats were not different among wild, physically sterilized, triploid, or diploid adults (Trested et al., 2011).

For CR SNS, there are three concentration reaches in the 198 rkm range (Kynard, 1997). The lowermost concentration reach (Connecticut) includes a long freshwater reach and the estuary (Buckley and Kynard, 1985a; Savoy, 2004). The other two upstream reaches (Agawam and Deerfield) are in fresh water and include both the mainstem and the lower reaches of large tributaries (Kynard et al., 2000, 2012a, b; Kieffer and Kynard, 2012a, b).

Within a concentration reach, summering occurs in saline water (GOM SNS) or in fresh water at the freshwater: saltwater zone (southern SNS). The exception among GOM rivers is the MR, where adult SNS can remain in fresh water all year like CR SNS, with some individuals (particularly, post-spawning adults) visiting saline water for short periods (1−6 wk) in late-spring

412 (Kieffer and Kynard, 1993; Kynard et al., 2012a; Savoy, 2004). Shortnose Sturgeon typically use
413 concentration reaches within the mainstem of rivers, but some CR SNS enter the lower 5−10 rkm
414 reaches of large tributaries to forage, but not to overwinter (Kieffer and Kynard, 2012b; Kieffer
415 and Kynard, 2012c). Tributary use has not been reported in other northeastern rivers.
416
417 **F. Verification of a spawning population**
418 Spawning populations throughout the range have usually been identified either by the presence of a
419 spawning run of mature adults or by the presence of young juveniles (< 1 yr, too young to be
420 tolerant of high salinity and whose movements are restricted to their natal river and estuary (Fig.
421 2). In addition to young juveniles indicating a spawning population exists, their presence indicates
422 recruitment may occur.
423 The capture of ELS and young juveniles remains the most convincing evidence of a viable
424 spawning population. Tracking the migration of pre-spawning adults alone, without capture of
425 ELS, is insufficient evidence to indicate successful spawning occurs. For example in the 1980s,
426 tracking pre-spawning adults in the reach just downstream from Holyoke Dam on the CR
427 suggested adults spawned at the dam (Buckley and Kynard, 1985b). However, later extensive
428 tracking of adults plus netting for ELS in the 1990s found the reach was not a major spawning site
429 and only a rare female spawned at Holyoke (Kynard et al., 2012b).
430 Young juveniles have been captured in rivers with only tens of spawning adults, i.e., in the
431 CR (Buckley and Kynard, 1983b; Kynard, 1997; Kynard et al., 2012a, e) and in the MR (10
432 juveniles, smallest, 47.5 cm TL; Kieffer, M., unpbl. data). The MR juveniles support the
433 conclusion of likely recruitment (Kieffer and Kynard, 1996; Kynard, 1997; Fig. 2).

Abundance of adults has also been used as a strong indicator of spawning success, particularly for rivers with tens of thousands of adults like the HudR (Fig. 3; Bain, 1997). However, recent tracking and genetic analysis of SNS from basins throughout the range indicates more coastal movement by SNS than previously recognized. Thus, throughout the range, the presence of a few adults in a river does not mean a spawning population is present. For example, the few fish observed in the Housatonic River, CT (Savoy, 2004) and in the Saco River, ME (Little et al., 2014; Wippelhauser et al., 2015) are non-natal wanderers foraging in non-natal coastal rivers. However, the situation may be different in the PotR, where all three captured adults were late-stage females and one female swam a one-step spawning migration to spawning habitat in Washington, DC, indicating the potential for spawning and the possibility of a natal remnant population or ongoing colonization by DelR adults (Kynard et al., 2009).

Migrant adult SNS entering rivers without a natal SNS population represent potential colonizers and they should be monitored carefully. Native populations of SNS were extirpated or reduced to a remnant population in many rivers, but if river habitats are available to complete their life history, coastal SNS migrants may find and colonize these rivers.

The situation in the MR is unclear because presumed natal adults spawn there (Kieffer and Kynard, 1996) and recently, telemetry-tagged adult SNS from other GOM rivers used the lower MR river to forage in summer, overwinter, and then, return in spring to the KenR to spawn (Kynard and Kieffer, 2009; Wippelhauser et al., 2015). This greatly complicates any attempt to determine abundance of natal non-spawning adults in the MR, which can only be done using the latest genetic techniques to identify half-sib offspring of a non-natal x natal mating. Given the recent and similar discovery of widespread inter-basin movements by adult southern SNS, estimating adult abundance in any river at any time except during spawning would always contain

457 an error (magnitude unknown) due to emigration (of natal adults) and immigration (of non-natal
458 adults).

459 ## Recruitment and Population Metrics

460 Gross et al. (2002) used elasticity analysis of SNS, AS, and White Sturgeon = WS (A.
461 transmontanus) to estimate the potential to increase population growth rate (recruitment) by
462 improving survival of yr-1 and older juveniles or increasing fecundity. Changes to fecundity had
463 little effect and the greatest potential to effect growth rate occurred with increased survival of
464 YOY. Gross et al. (2002) did not examine the role of increased survival of free embryos or larvae
465 on recruitment rate. However, survival of these life stages in the artificial stream of Kynard et al.
466 (2012e) during 7 yr suggests year class strength may be established earlier than the YOY life stage,
467 perhaps in the larval stage or at least by the time larvae develop into juveniles. If correct, increased
468 protection of ELS in rivers is critical to increasing recruitment, adult abundance, and successful
469 sturgeon restoration in many rivers.

470 Population metrics for SNS throughout the range was described by Dadswell et al. (1984).
471 Maximum age of SJohnR was 32 yr for males and 67 yr for females. Age structure of the upstream
472 segment CR SNS was done by Taubert (1980b), who estimated a maximum age for adults of 34 yr.
473 All aging in these studies was done using non-validated fin ray sections.

474 After these studies, the inaccuracy of aging CR SNS using fin sections stopped population
475 metrics studies on the population. In 1982, researchers using pectoral spine sections and techniques
476 like Taubert (1980b) from 69 adult downstream segment CR SNS found fish were 8−29 yr
477 (Buckley and Kynard, 1983a). However, there was poor (≤50%) agreement between two fin
478 section readers. Errors were particularly great for older fish, where marginal rays were eroded or
479 absorbed during wintering (Buckley, J. and Kynard, B., unpbl. data). These results were never

480 published. Similar results were found by Savoy, T. (CT Dep. Energy and Environ. Prot., unpbl.
481 data) when aging tens of downstream segment CR SNS. In addition, several CR adults with a
482 pectoral fin section removed by Taubert (1980b) were recaptured after a few years and their fin
483 spines had healed poorly. Observing the swimming ability of these fish in holding tanks clearly
484 showed the deformed fins affected swimming and foraging ability (adults were thin with a low CF;
485 Kieffer, M. and Kynard, B., unpbl. data). Removing spine sections would not provide reliable data
486 on adult age (Buckley and Kynard, 1983b), and further, deleteriously affected swimming ability.
487 Thus, B. Kynard (CR SNS permit holder) consulted with NMFS Protected Species and removal of
488 fin sections from CR SNS was discontinued in 1982. Recent aging of adults ≥ 6 yr in southern
489 rivers also found inaccuracy using pectoral spine sections (Post, W.., SC Dep. Nat. Resour.,
490 Charleston, SC, pers. comm.). Thus, even in short-lived southern SNS, aging of adults is
491 inaccurate. Another aging method is needed for SNS population dynamics modeling.
492 For CR SNS, instead of aging fish using pectoral fin rings, researchers separated captured
493 fish into juvenile and adult size classes using the smallest size of adults at the spawning grounds or
494 running sperm to characterize the adult stage. Juveniles were smaller fish (Kynard et. al., 2012a, b;
495 Kieffer and Kynard, 2012a). In the CR, the smallest mature males were 69.0 cm TL (1.4 kg) and
496 the smallest mature females were 73.0 cm TL (2.3 kg). This size compares closely with the
497 smallest known mature female captured in the PenobR (70 cm TL and 2.5 kg; Kinnison, M., pers.
498 comm.) and also, with SNS from southern rivers (Peterson, D., unpbl. data).
499 **A. Age structure**
500 Age structure of SNS has not made any progress due to the problem of accuracy of aging fish.
501 Inaccuracy using fin sections is probably most acute in long-lived northern populations. Although
502 Dadswell (1979) did not find a strong indication of year class failures in the SJohnR population

503 using fish age determined from pectoral spine sections, monitoring annual spawning success of CR
504 SNS for 17 yr found the opposite result. Occasionally, there was a complete spawning failure year
505 (zero year class) and further, a year of major successful spawning only occurred at about every 10
506 yr (Kieffer and Kynard, 2012a). Perhaps, Dadswell (1979) did not discover differences in year
507 class strength because of errors in aging adults using fin rays. Failure of SNS year classes also
508 occurs in southern rivers, like the AltR (Peterson, D., unpbl. data), so this phenomenon occurs
509 throughout the species range. A lack of proper aging techniques and the inability to include annual
510 recruitment failure in models makes present population recruitment and growth models inaccurate.
511 Researchers have found it impossible to accurately age adult CR SNS using fin ray spines,
512 yet the SNS age information derived from fin rays by Dadswell (1979) continues to be used
513 (Usvyatsov et al., 2012b). There is a great need to verify the accuracy of this information.
514 In 2011 hundreds of CR SNS representing 15 year classes reared throughout life in ambient
515 river temperature were euthanasized for aging and other research (Kynard, B., unpbl. data).
516 Otoliths, fin ray sections, and other tissues were provided to many researchers studying aging.
517 These known-age juveniles and adults could provide critical information on the accuracy of
518 various techniques for determining age of northern SNS.
519
520 **B. Sex ratio**
521 A latitudinal difference in sex ratio was suggested by the 2:1 female: male sex ratio in the SJohnR
522 compared to the 1:1 ratio in the GPeeDR, SC (Dadswell et al., 1984). One other sex ratio pattern
523 was present in the SJohnR, where the ratio was 1:1 (female: male) among juveniles, but 2:1 among
524 adults, suggesting more males than females die as they age, i.e., females have a longer life
525 expectancy (Dadswell, 1979). The sex ratio of CR adults is about 1:1 (Kieffer, M. and Kynard, B.,

526 unpbl. data). Latitudinal sex ratio needs further study.

527 Identification of the sex of individual SNS has been observed using many techniques, but use
528 of a borescope to sex CR SNS greatly improved the accuracy of sexing CR females any time of the
529 year (Kynard and Kieffer, 2002). However, the technique did not improve accuracy of identifying
530 males (Kynard et al., 2012b). Methods for improving sex determination and staging of sexual
531 maturity for SNS continue to be developed (Matsche et al., 2012a).

532

533 **C. Sexual dimorphism**

534 Old adult females in all rivers grow heavier with age compared to males (Dadswell et al., 1984).
535 However, no external character or suite of characters has been found to identify the sex of 100% of
536 the adults. Even experienced researchers can make a mistake identifying the sex of a pre-spawning
537 adult. For example in the early 1990s, the annual accuracy of identifying CR males using external
538 characteristics was found in later years to be only 75−100%, and for females, the accuracy was less
539 (67−100%; Kynard et al., 2012b). However, using a borescope to observe ovaries resulted in 100%
540 of adult females being identified correctly (Kynard and Kieffer, 2002). Virgin mature females are
541 most easily confused with males or non-mature females; particularly, if a slim female squirts
542 ovarian fluid that resembles a male's milt (Kieffer, M., unpbl. data).

543

544 **D. Growth and length-weight relationship**

545 Males and females from the Bay of Fundy and the CR have similar growth relationships, with
546 SJohnR males growing faster than females until mature. Thereafter, male growth rate slows more
547 rapidly than that of females (Dadswell, 1979). A similar situation occurs in the growth of marked

upstream segment CR adults recaptured over 17 yr: male growth is slow compared to females (Kynard et al., 2012a).

Shortnose Sturgeon populations vary widely for condition factor = CF (length-weight relationship) with dam-locked segments upstream of dams (regardless of river system) having the lowest CF. The dam-locked CR segment had the lowest CF of all adults examined by Dadswell et al. (1984) or later by Kynard et al. (2012a). Not surprisingly, the CF of the dam-locked upstream CR segment is similar to the dam-locked segment of SNS in the Santee R (Collins et al., 2003). Dadswell et al. (1984) also reported the KenR population had a low CF, but this was not studied further. The low CF of SNS restricted to only fresh water shows the adaptive significance for increased growth and condition during a diadromous life style. This situation is commonly observed among sturgeons (Holcik, 1989).

E. Age at maturity

The age at maturity is earliest in southern populations and latest in Bay of Fundy, GOM, and northeastern populations (Dadswell et al., 1984). Typically, southern females are estimated to mature at age 3−4 yr, and northern females estimated to mature at 10−12 yr. The maturity estimate for northeastern females may be inaccurate by a few years (Kynard, B., unpbl. data). Most males likely mature a year or more earlier than females. The spawning strategy hypothesis for northern vs. southern SNS follows: northern SNS must live many years, presumably, because annual spawning success (or rearing success of ELS) is less predictable than for southern SNS (Kieffer and Kynard, 2012a). However, data on long-term annual spawning success is available for the CR (Kieffer and Kynard, 2012a), but lacking for all southern rivers, so the hypothesis cannot be tested, yet.

Adults likely spawn throughout life (Kynard et al., 2012a, c; Kieffer and Kynard, 2012a). However, the post-reproductive period could be a time of increased mortality for old fish. Two maximum-size CR males were found dead at the spawning site immediately after spawning ceased (Kynard, B., unpbl. data).

F. Latitudinal differences in population metrics

Southern SNS exhibit several latitudinal differences in life history traits compared to their northern counterpart (Kynard, 1997). For example, southern SNS grow faster, mature at a younger age, and have a shorter lifespan (Dadswell, 1979; Dadswell et al., 1984). This pattern is similar between southern Gulf Sturgeon = GS (A. oxyrinchus desotoi) and northern AS. Shortnose Sturgeon was reported to mature at 50−60 cm TL by Vladykov and Greeley (1963), but this estimate is incorrect for CR SNS, which mature at a larger size (69 cm TL for males; Kynard, 1997). In the Bay of Fundy, GOM, and northeastern populations, males may grow to a mature size in 5−6 yr, and females grow to a slightly larger maturity size (73 cm TL) in 8−12 yr. In contrast, maturity in southern populations is reached by males in 2−3 yr and by females in 3−5 yr (Dadswell et al., 1984). Shortnose Sturgeon live an estimated 67 yr in the SJohnR (Dadswell et al., 1984) to 34 yr in the CR (Taubert, 1980b), and <20 yr in the South (Dadswell et al., 1984; Rogers and Weber, 1994a; Cooke et al., 2004). All ages cited in the studies were determined by fin ray sections, the accuracy of which is suspect, particularly for northern SNS (see Age structure section).

Additionally, northern SNS grow larger than southern SNS (Dadswell et al., 1984). A maximum size of northern females (143 cm TL, 23.6 kg weight) and northern males (108 cm TL, 9.4 kg weight) was reported by Dadswell et al. (1984). However, maximum size of northern males may be even larger in some GOM and northeastern rivers, i.e., 128 cm TL for a MR male captured

in 2011 (Kieffer, M., unpbl. data) and 10.7 kg for a downstream segment CR male captured in 1997 (Savoy, T., unpbl. data). Southern adult SNS also have a shorter maturity cycle between spawning than northern adults (Dadswell, 1979; Kynard, 1997).

Throughout the range, males typically spawn every 1−2 yr and females typically spawn every 3−5 yr (Dadswell, 1984). Recent studies on CR and MR males found many males spawned annually but females varied greatly for spawning interval (Kieffer and Kynard, 2012a; Kieffer, M., unpbl. data). It seems likely that many southern males spawn annually.

Connecticut River SNS adults (and probably, adults in other northern rivers) lose body weight during the long (5 mo), cold wintering period (Kynard et al., 2012a). Also, AltR SNS lose weight during the summer, when warm temperatures and low DO levels in fresh water stress fish (DeVries and Peterson, 2006). A similar decrease in body weight during trophic dormancy is found in GS (dormant season in rivers, spring, summer, fall; Sulak and Clugston, 1999). Seasonal movements suggest that mid-Atlantic and southern SNS use brackish and marine estuarine habitats as their primary feeding areas, particularly during the fall-winter months (DeVries and Peterson, 2006; Kynard et al., 2009).

G. Abundance estimates

The use by SNS of several concentration reaches in a natal river poses special problems for estimating the total number of adults in the population. This problem applies to any sturgeon species that spends time in concentration reaches in their natal river and estuary. For example, the adult estimate of 1600−1800 adults in the downstream segment CR SNS is likely valid only because marked and recapture of adults occurred at one concentration reach for many years (1988−2002) giving SNS in the other concentration reaches and at Holyoke Dam time to move to

617 the one reach sampled. Immigration of non-natal SNS into the CR also is low (Savoy, 2004).

618 The best time to estimate abundance of SNS is during an aggregation period, when
619 emigration and immigration are at their lowest level. Shortnose Sturgeon adults in all stages of
620 reproduction aggregate during refuge seeking: summer in the South and mid-Atlantic rivers and
621 winter in northern rivers (northeastern, GOM, and Bay of Fundy). If all refuge aggregation sites in
622 a natal river are known, and immigration of non-natal adults is known, abundance at each refuge
623 reach can be estimated using traditional drift gill net and mark-recapture or by underwater video
624 surveys (Li et al., 2007; Usvyatsov et al., 2012b; Kieffer and Kynard, 2012b).

625 If gill-netting and mark recapture is used, this should be done prior to river temperatures
626 decreasing to 7°C. If colder, wounds on northern SNS will not heal all winter (Kynard, B., unpbl.
627 data). The same goes for incisions during internal telemetry tagging (Kieffer and Kynard, 2012d).

628

629 ## Habitat Requirements, Preferences, Foraging, and Tolerances

630 ### A. Latitudinal pattern of freshwater: saltwater use

631 The degree of anadromy (relative use of fresh water versus salt water) varies in a complex way
632 with latitude (Kynard, 1997). Across the range, SNS in the Bay of Fundy, GOM, and southern
633 rivers use salt water particularly, the freshwater: saltwater zone, much more during their life
634 history than do SNS in northeastern rivers (CR, HudR, and DelR) and in the MR, the most
635 southern river in the GOM. A characteristic feature of SNS in northeastern rivers that is shared by
636 MR SNS is their extensive use of fresh water to forage and overwinter. This use of fresh water
637 makes MR SNS different from other SNS located geographically in the GOM, which extensively
638 use salt water (Kynard, 1997; Kieffer and Kynard, 1993; Wippelhauser et al., 2015).

639 Kynard (1997) proposed a hypothesis to explain the latitudinal pattern of saltwater use by
640 SNS, i.e., that the degree of saltwater use may be related to bioenergetic adaptations to use
641 freshwater or saltwater habitat to optimize foraging and growth. The basic observation follows:
642 older juvenile and adult SNS in GOM rivers spend less time than northeastern SNS foraging in
643 freshwater, SNS in northeastern rivers spend the most time foraging in fresh water, and southern
644 SNS forage mostly at the freshwater: saltwater zone or in saltwater. This use of freshwater habitat
645 suggest the following hypothesis: river conditions (particularly, thermal regime) and forage
646 abundance needed for good growth in fresh water are poor in the Bay of Fundy, poor in northern
647 GOM rivers, best in northeastern rivers, and worst in southern rivers.
648 Kieffer and Kynard (1993) termed the pattern of freshwater: salt water use by MR SNS as
649 freshwater amphidromous, a term applied to fish that spawn in fresh water, but visit salt water to
650 forage during some period of life (McDowall, 1988). With recent additional information on fresh
651 water and salt water use by SNS throughout the range, it still seems appropriate to characterize
652 SNS as amphidromous, with use of salt water depending on river location within the range.
653 Adaptive significance of the short visits to saline water in spring by adult northeastern SNS and by
654 MR adults is not known, but one hypothesis follows: fish visit salt water on individual schedules
655 depending on their need to forage in saline water to obtain minerals that are limited in fresh water
656 (Kieffer and Kynard, 1993).
657
658 **B. Home and foraging ranges**
659 The total length of river and estuary used (home range) is highly variable among populations. Most
660 northeastern populations typically use about 200 rkm of river (Kynard, 1997). Some southern
661 populations travel far upstream to find rocky spawning substrate, for example, SNS in the AltR

662 (Devries and Peterson, 2006). Because the spawning site is the most upstream reach used by SNS
663 in any river yet studied, Kynard (1997) speculated that the variability in linear range among rivers
664 may indicate how far upstream adults must swim to find suitable rocky or rough, clay bits on the
665 river bottom for spawning. This distance would be farther in southern rivers because of the
666 difference in width of the coastal plain: narrow in GOM and northeast and wide in the South.
667 Telemetry tracking of free-swimming MR SNS found the mean foraging range was 6.7 rkm,
668 which is similar to the mean foraging range of upstream segment CR adults (8.4 rkm; Kieffer et. al,
669 2012b). The similarity of foraging range size between MR adults (total estimated abundance = 37
670 adults) and upstream segment CR SNS (total estimated abundance = 328 adults) suggests size of
671 the SNS foraging reach in northeastern rivers is independent of adult density up to a density of
672 seven adults/rkm.
673 The freshwater distance used for the foraging range increases with ontogenetic life stage of
674 northeastern SNS. The mean foraging range (2.2 rkm) of four juvenile CR SNS was significantly
675 smaller ($P < 0.01$) than the mean range (6.7 rkm) of 15 CR adults (Kieffer et al., 2012b). This
676 suggests an ontogenetic increase in foraging range with an increase in body size (age). Also, the
677 study found the mean wintering range of CR adults was 0.8 rkm, which is larger than the wintering
678 range of juveniles (0.2 rkm).
679 Size of the foraging range of two PotR SNS adult females was 78 rkm, suggesting SNS in
680 mid-Atlantic rivers utilize a larger foraging range than northeastern SNS (Kynard et al., 2009).
681 Also, range size of PotR SNS was largest in fall and spring and smallest in late-summer and
682 winter. For southern SNS feeding in the river, benthic prey may be more available in winter than in
683 summer, as was found in the Suwannee River (Mason and Clugston, 1993).
684 Foraging range has not been extensively studied in southern rivers, but telemetry tracking of

SavR adults found they used only a 19 rkm reach in the lower river, which included the freshwater: saltwater zone (Griggs, 2003; Trested et al., 2011). The smallest daily range occurred in spring (1.7 rkm) compared to a larger range (3.8 rkm) in winter. The difference in seasonal range size may be related to seasonal changes in salinity. A similar situation exists in other southern rivers (Flournoy et al., 1992; Rogers and Weber, 1994a, b; Collins, M., unpbl. data). Also, data from telemetry tracking, seasonal changes in condition factor of SNS, and gastric lavage indicated most foraging in southern rivers occurred during fall to spring (Collins, M., unpbl. data). During the coolest months of the year, when the foraging range of southern SNS expanded, fish moved from the freshwater: saltwater zone into higher salinity regions of the estuary where intensive foraging occurred (Hall et al., 1991; Moser and Ross, 1995; Rogers and Weber, 1995).

C. Foraging habitat by life stage

In two northeastern rivers (DelR and HudR) with SNS and AS populations, ELS of both species begin life in freshwater. However, with increasing age, juvenile AS move downstream to more saline habitat, whereas SNS larvae and juveniles remain in freshwater tidal habitat (Bath and O'Conner, 1981; Brundage and Meadows, 1982; Haley et al., 1996; Bain, 1997). Before sturgeon abundance was reduced by anthropogenic forces in these and other northeastern and GOM rivers, the tidal reach provided rearing habitat for both species of sturgeons, which were likely a major component of the benthic fish community.

Foraging habitat by life stage is not well understood throughout the range, particularly for larvae and YOY. Larvae are the first foraging life stage and dispersing northeastern larvae are near the channel bottom in the CR and the HudR (Taubert, 1980a; Bath and O'Conner, 1981). Kynard and Horgan (2002a) found dispersing CR larvae used the bottom meter of the water column in an

artificial stream, which corresponds well with capture locations of wild HudR and CR larvae (Bath and O'Conner, 1981; Taubert and Dadswell, 1980). After larval dispersal stopped, CR larvae in artificial streams foraged on open sand substrate (Kynard and Horgan, 2002a). In all rivers, larvae and YOY have only been collected in fresh water downstream from spawning areas (Taubert, 1980a; Taubert and Dadswell, 1980; Bath and O'Conner, 1981; Kynard et al., 2012b; Kieffer and Kynard, 2012a).

There is poor understanding on habitat use of wild YOY in any river during summer-fall foraging, and later, during wintering. Artificial stream studies of YOY SNS in fall, winter, and spring found fish selected the fastest velocity available but were very broad in bottom habitat preference as they had no preference for sand vs. cobble rock habitat in any season (Kynard et al., unpbl. data). The adaptive significance of these preferences is not known but pose interesting hypotheses.

Juveniles (yr-1+) and adults forage together over sand and sand−mud (Dadswell et al., 1984; Dovel et al., 1992; Savoy and Benway, 2004). Connecticut River yr 1−2 juveniles also foraged over sand with adults, suggesting that juveniles as young as yr-1 use the same habitat as adults (Kynard et al., 2000). Riverine habitats typically used by juveniles and adults follow: sandy to hard-mud bottom; water depth − highly variable from channel to shoals, with night-time foraging often in water <1 m deep; but no diel pattern of water depth use by CR SNS (Kynard et al., 2000). However, SJohnR SNS have a seasonal difference in foraging depth where the shallowest depths are used in the fall (Usvyatsov et al., 2012c). Thus, GOM and northeastern SNS are highly flexible for foraging depth with fish probably going wherever forage is most abundant.

D. Diet by life stage

There are limited observations on SNS larval feeding, but SNS is likely similar to other sturgeon larvae and forage on any suitably-sized small benthic zooplankton and invertebrates (Muir et al., 1988). Early-larvae have many teeth (9−12 upper jaw and 8−11 lower jaw; Dadswell et al., 1984; Snyder, 1988), so fish can grasp and hold prey. Buckley and Kynard (1981) observed CR SNS larvae actively chasing and grasping zooplankton in an artificial tank, so fish were using vision to chase prey. Their large mouth (Snyder, 1988), should give them a wide choice of forage items. Kynard and Horgan (2002a; Kynard et al., 2012c; Parker and Kynard, 2014) found SNS larvae dispersed mostly at night, a diel behaviour further suggesting vision is important for daytime foraging. Further, both CR larvae and larvae of Kootenai River WS foraged mostly on drift (Kynard and Horgan, 2002a; Parker and Kynard, 2014; Kynard et al., 2013, 2014a). This foraging strategy requires excellent vision to succeed.

Diet of SNS YOY is poorly studied, but feeding on drift (like larvae) may be common. Dead HudR YOY impinged on power plant intakes had been foraging on various species of benthic invertebrates like dipteran larvae, amphipods Gammarus, and isopods Cyathura (Carlson and Simpson, 1987). The dipteran prey of YOY was the dominant dipteran in the drift, but was not the dominant dipteran on the channel bottom, where YOY were located (Dovel et al., 1992). This difference suggests YOY were foraging mostly on drift and not on benthos. Drift feeding by YOY SNS and has been observed in artificial streams (Parker and Kynard, 2014; Kynard, B., unpbl. data) and also observed on YOY WS (Kynard et al., 2013, 2014b) suggesting YOY from diverse sturgeon species forage on drift. During drift feeding, YOY hold position on the bottom or behind a bottom velocity refuge and feed on food items that drift to them. Drift feeding by larval and YOY juvenile sturgeons may be a widespread foraging behaviour.

753 Juveniles and adults are characterized as benthic cruising predators with a broad diet,
754 foraging opportunistically on a wide variety of invertebrates like benthic insects, crustaceans,
755 mollusks, and polychaetes (Taubert, 1980b; Dadswell et al., 1984; Kynard, 1997; Usvyatsov et al.,
756 2012c). Forage items vary widely depending on their abundance in space and time. Abundant
757 evidence for this foraging style was reported by Dadswell et al. (1984), Carlson and Simpson
758 (1987), Savoy and Benway (2004), and Kieffer and Kynard (unpbl. data). Shortnose Sturgeon
759 locate prey using vision, barbels (tactile and taste receptors), electroreceptors, or a combination of
760 senses, and then, grasp prey on the bottom (or off plant surfaces; Dadswell et al., 1984) with their
761 protuberant mouth. Fish in all foraging life stages grasp drifting or benthic prey with their jaws and
762 do not vacuum food off the bottom as many biologist believe.
763 Mollusks seem to be a major forage item as SNS age. There is a trend with age of SJohnR
764 SNS to forage more on mollusks, both pelecypods in the benthos and gastropods on vegetation
765 (Dadswell, 1979). Evacuated stomachs of many upstream segment CR adults contained mostly
766 freshwater mollusks with a maximum length of 3.5 cm (Kieffer and Kynard, unpbl. data).
767 The diet of adult SNS typically consists of small bivalves, gastropods, polychaetes, and even
768 small benthic fish (McCleave et al. 1977; Dadswell, 1979; Dadswell et al., 1984; Moser and Ross,
769 1995; Bain, 1997; Savoy and Benway, 2004; Usvyatsov et al., 2012c). Both juveniles and adults
770 primarily forage over sandy or sand-mud bottoms that produce abundant benthic invertebrates
771 (Carlson and Simpson, 1987).
772 The large alimentary gizzard is believed to be an adaptation to crush mollusk shells, but
773 almost all bivalve shells (each, 30-35 mm long) exiting from 15 wild CR adults held in tanks after
774 capture were intact (but open) when expelled from the anus. Thus, the gizzard did not crush the
775 shells; instead, digestive fluids may have caused the mollusks to open. However, fragments of

776 shells have been removed from inside gizzards during dissection of both SNS and AS (Hilton, E.,
777 unpbl. data). Thus, it is possible that passing whole shells of CR SNS was due to the stress of
778 capture. In addition to foraging on native bivalves, adults forage on invasive mollusks. The
779 invasive zebra mussel (Dreissena polymorpha) is a major forage item of adult SNS in the HudR
780 (Bain, M., Cornell Univ., Ithaca, NY, unpbl. data). Further, adult MR SNS forage on young (11
781 mm long) invasive Asian clam, Corbicula fluminea (Kieffer, M., unpbl. data), a previously
782 unreported food item. In contrast, Savoy and Benway (2004) did not find downstream segment CR
783 SNS adults foraged on Asian clams even though these bivalves were the most abundant mollusk at
784 one of their sampling reaches. Similarly, Asian clams are common in the SavR and EdisR, but
785 recent diet studies found they were not eaten by SNS (Collins, M, unpbl. data). Perhaps, hard-
786 shelled mollusks are only eaten when more preferred soft-bodied prey is low in abundance.
787 Shortnose Sturgeon yr-1 juveniles to adults seem highly adapted to a wide ecological
788 variation in physical factors during foraging. The diel cycle (day versus night) or tidal cycles (ebb
789 versus flood) did not affect movement direction or distance moved upstream or downstream
790 between foraging habitats of SNS in the CR or MR (Kieffer et al., 2012). McCleave et al. (1977)
791 also found no relation between foraging movements of SNS in a Maine estuary relative to tidal
792 cycle.
793
794

795 **E. Habitat fragmentation**

796 The lowermost dam in many rivers throughout the species range blocks upstream migration to
797 spawning and rearing reaches (review by Kynard, 1997). In the Bay of Fundy and in most GOM
798 and northeastern rivers (PenobR, KenR, AndroR, SJohnR, MR, CR, and HudR) dams have

799 blocked upstream migrations (Dadswell et al., 1984; Kynard, 1997). In the Susquehanna River and
800 large rivers in VA and NC, damming likely was a major factor causing the extirpation of SNS
801 populations. Rivers with known effects of dam blockage on SNS in the South are the SantR
802 (Cooke and Leach, 2004) and CapFR (Moser and Ross, 1995).

803 While damming likely affects SNS throughout the range, the long-term studies on CR SNS at
804 two dams provide the best understanding on the multiple effects of damming that divides
805 (segments) a SNS population.

806 The situation for the segmented CR SNS was discussed under northeastern rivers, but is
807 briefly reviewed here as not all details were covered previously. The upstream segment of CR SNS
808 (328 adults + all other life stages; Kynard, 1997) is upstream of Holyoke Dam, completed in 1849.
809 The upstream segment uses a large foraging−wintering concentration reach (Deerfield) plus a
810 small spawning reach, Montague, which is the most upstream reach used. After adults have
811 spawned is the only time when there is a major adult downstream migration to the downstream
812 concentration reaches and the estuary (Kynard et al., 2012a; Kieffer and Kynard, 2012a). About
813 50% of the juveniles produced by the upstream segment migrate downstream past Holyoke Dam to
814 the downstream segment during the spring-fall as yearlings---this is the main connection between
815 the two segments. Upstream segment SNS do not use the 7-rkm long reservoir upstream of
816 Holyoke Dam except as a migration route, so damming only caused the loss of about 7 rkm of SNS
817 river habitat. The downstream CR SNS segment (downstream of Holyoke Dam) is estimated at
818 1600−1800 adults (Savoy, 2004). These adults (and juveniles) can forage in the estuary and lower-
819 river, but the summer upstream migrations by juveniles, non-spawning adults, and pre-spawning
820 staging adults to Deerfield and the spring upstream migrations by juveniles, non-spawning adults,
821 and pre-spawning adults are blocked by Holyoke Dam. Thus, only a rare female (1 of 19 tracked

822 females; Kynard et al., 2012b) spawns at Holyoke. Without upstream passage at Holyoke Dam, no
823 juvenile or adult in the downstream segment can complete their natural life migrations and spawn
824 at Montague (Kynard, 1998; Kynard et al., 2012a, e).

825 After an estimated more than seven CR SNS generations (160-yr post damming),
826 downstream segment juveniles and adults continue upstream non-spawning, pre-spawning staging,
827 and pre-spawning migrations that should lead to accessing the upstream concentration reach
828 (Deerfield) and completion of a natural life history (Kynard et al., 2012e). Extensive comparison
829 of substrate and velocity at Holyoke Dam with other known sites where SNS spawn in the CR and
830 in two other rivers, found there is abundant presumptive spawning habitat just below the dam that
831 is not used (Kynard et al., 2012b), so females apparently are genetically programmed to home and
832 spawn at the upstream historical grounds (Rock Dam reach) at Montague.

833 Holyoke Dam segmented the SNS population by blocking upstream migrations to the
834 historical concentration reach for foraging, wintering, and spawning, and additionally, killing and
835 injuring downstream migrant juveniles and adults when they pass downstream of the dam (22 of
836 49 tagged adults died while passing the dam; Kynard et. al, 2012a). Thus, both segments are
837 maintained by spawning of a few upstream segment adults and the annual downstream migration
838 by yr-1 juveniles from the upstream segment (Kynard et al., 2012a, d, e).

839 The large number of adult SNS in the downstream segment is a reproductive null without
840 upstream fish passage at Holyoke Dam that enables these adults to spawn at the historical grounds
841 at Montague (Kynard, 1998; Kynard, 1997; Kynard et al., 2012a). Holyoke Dam was built on a 5
842 rkm-long rapids, which historically, separated the upstream concentration reach from the two
843 downstream concentration reaches. Because these rapids are only used as passage routes and not
844 for spawning, the greatest impact of damming has been to block the upstream migration route for

juveniles and adults to Deerfield and Montague and killing upstream segment migrant SNS when they pass through turbines at the dam. All data suggests a similar situation exists in a dammed southern river, the SantR (Finney et al., 2006).

F. Seasonal refuge

Shortnose Sturgeon use river and estuarine reaches as refuge places, which are small reaches within the larger concentration reach or home range (Northcote, 1978). Refuge reaches are used to survive seasonally extreme environmental conditions. In GOM and northeastern rivers, the severe conditions occur during the 5 mo wintering period as a result of low temperatures during winter. In mid-Atlantic and southern rivers, the severe conditions occur during the summer, when temperatures are warm and dissolved oxygen = DO levels are low (see Internal Biology Section). Use of summer refuge reaches by GS seem related to energetic conservation (Sulak et al., 2007), which may also be significant for southern SNS.

Conservation of energetic resources to survive the long winter is the most likely explanation for the sedentary behaviour and selection of habitat by northeastern and GOM SNS (Kieffer and Kynard, 2012b). In the Bay of Fundy, GOM, and in the MR, wintering sites are in fresh water, often just upstream of the freshwater: saltwater zone. A summary of rivers and references on wintering refuge follow: SJohnR – Dadswell, 1979; Li et al., 2007; Usvyatsov et al., 2012b; KenR – Squires and Smith, 1980; PenobR – Fernandes, 2008; Fernandes et al., 2010; MR − Kieffer and Kynard, 1993; Kieffer, M., unpbl. data; CR − Buckley and Kynard, 1985a; Kynard et al., 2000; Savoy, 2004; Kieffer and Kynard, 2012c; Wintering reaches in northeastern rivers are variable with aggregations of juveniles and adults in fresh water just upstream of the freshwater: saltwater zone to aggregations far upstream from salt water -- HudR – Dovel et al., 1992; Bain, 1997; DelR

868 – Hastings et al., 1987; O'Herron et al., 1993; Brundage and O'Herron, 2009; Env. Res. and
869 Consult., 2006; CR – Buckley and Kynard, 1985a; Savoy, 2004; Kieffer and Kynard, 2012c).
870 The number and location of wintering reaches can vary annually. The number of reaches
871 used in CR, MR, and DelR SNS is not related to population abundance or length of the river range
872 (Kieffer and Kynard, 2012c). Instead, the number of wintering reaches is probably a local adaption
873 to each river system and may be related to density of SNS. The wintering reach for SJohnR SNS in
874 the Kennebecasis River (Usvyatsov et al., 2012b) was not in the more saline location used by
875 wintering adults in the 1970s (Dadswell, 1979). Use of different wintering sites among years has
876 also been observed in the CR and MR, but the cause for these changes is not understood (Buckley
877 and Kynard, 1985a; Kieffer and Kynard, 1996; Kieffer and Kynard, 2012b; Kieffer, M., unpbl.
878 data).
879 Environmental factors triggering fall movement to wintering reaches and spring departure
880 from wintering reaches has been studied in the CR where movements of SNS to and from
881 wintering reaches were closely correlated with day length (photoperiod), not with river
882 temperature or discharge (Kieffer and Kynard, 2012c). Most CR adults and large juveniles move to
883 a wintering reach in fall when day lengths are 9.82–9.60 h; and in spring, most fish depart
884 wintering reaches when day length is 13.37–13.77 h. Thus, the wintering period for CR SNS is 20
885 wk or 38% of the year (mid-November to mid-April).
886 Wintering habitat and behaviour of wintering SNS has been studied for years in the CR
887 (Kynard et al., 2000; Kieffer and Kynard, 2012c; Kieffer et al., 2012b) and recently, in the
888 Kennebecasis R., tributary of the SJohnR (Li et al., 2007; Usvyatsov et al., 2012b) and the
889 PenobR, a GOM river (Fernandes et al., 2010). In all rivers, SNS aggregate in winter, forming
890 dense aggregations in deep water. The function of this aggregation is not understood, but may be a

social response to stress because stressed SNS aggregate in other situations (Kynard, B., unpbl. data).

Characteristics of wintering reach use follow. Number of wintering reaches in the upstream 82 rkm of the CR, SNS adults (in all maturity stages and juveniles ≥yr 1) is six discrete wintering reaches (size range, 2.0−7.4 ha; Kieffer and Kynard, 2012c). Further, wintering reach fidelity of tracked CR adults during two consecutive years was 81.4%; thus, most SNS returned to the same reach each winter (Kieffer and Kynard, 2012c). Also, most CR adults do not move between reaches during winter (Buckley and Kynard, 1985a; Kieffer and Kynard, 2012c). DelR adult SNS utilize two discrete wintering reaches with most fish concentrated in the upstream 12 rkm of the upstream freshwater tidal reach, but a few are in 50 rkm of the lower tidal reach (O'Herron et al., 1993; Environ. Res. and Consult., Inc., 2006; unpbl. data). Juveniles in the DelR may overwinter in a more dispersed distribution throughout the tidal river reach (Brundage and O'Herron, 2009).

Underwater video found YOY are absent at the winter reaches used by older CR juveniles and adults, suggesting YOY have a different wintering strategy (and wintering reach; Kieffer and Kynard, 2012c). However, artificial stream studies with YOY CR and WS found activity level of both species decreased to almost zero at typically low winter temperatures ≤2°C (Kynard et al., 2013), which is similar to the activity level of older juveniles and adults (Kieffer and Kynard, 2012c). Thus, YOY activity level suggests an energy conservation strategy for wintering YOY like older SNS. Perhaps, YOY avoid wintering sites with adults to avoid being eaten by adults (Kynard, B., unpbl. data). Savoy and Benway (2004) found the few wintering CR SNS that contained food were juveniles <60 cm TL, suggesting juveniles actively foraged more than adults during wintering. Energetic factors may be responsible for small YOY selecting a wintering reach that provides greater opportunity for foraging, much like YOY GS during summer, which continue to

914 disperse into new river habitat all summer to forage (Kynard and Parker, 2004; Sulak et al., 2007).

915 Microhabitat in the wintering refuge of SNS has been studied in two rivers: the CR and the
916 Kennebecasis River. Connecticut River adults used curve and run reaches and selected
917 microhabitat with sand substrate, a bottom velocity of 0.07−0.96 $m \cdot s^{-1}$, and deep (but not the
918 deepest) water depths of 4.0–8.8 m (Kieffer and Kynard, 2012c). During periods of high river
919 discharge spikes, wintering adults moved slightly into slower velocity to conserve energy (Kieffer
920 and Kynard, 2012c). Kennebecasis River adults also selected sandy habitat, but they selected the
921 deepest sites (3−7 m; Li et al., 2007), not just a deep site like CR SNS. Selection of deep water for
922 wintering habitat has been reported for other sturgeon species (Berg, 1948; Bruch, R., Wisconsin
923 Dep. Nat. Resour., unpbl. data) and is likely related to avoiding high water velocity but remaining
924 in a velocity that may bring drifting food to you.

925 Behaviour of wintering SNS has been characterized in the CR. Behaviour of yr-2 juveniles to
926 adults follows: positively rheotactic and thigmotactic, stationary but not immobile, and alternated
927 resting on the bottom with slow in-place swimming (Kieffer and Kynard, 2012c). Where many
928 (hundreds) of wintering SNS were present, adults and juveniles aggregated closely together
929 (nearest-neighbor distance = one body width).

930 Southern SNS populations have a period of zero or reduced movement during summer refuge
931 use, which may be a response to high water temperature, low DO, salinity intrusion, energy
932 conservation, or all or a combination of some of these factors. For adult GS, the reduced summer
933 movement is related to energetics (Sulak et al., 2007). However, YOY GS do not use a summer
934 refugia, suggesting refugia use is specific to life stage in this species. During the summer, southern
935 adult and juvenile SNS from all rivers studied use the deep reaches of the freshwater: saltwater
936 zone or the estuary (Flournoy et al., 1992; Rogers and Weber, 1994a, b; Rogers and Weber, 1995;

937 Weber et al., 1998; Griggs, 2003; Devries and Peterson, 2006; Trested et al., 2011; Collins, M.,
938 unpbl. data). In the summer, SNS in the PotR (mid-Atlantic region) were stationary in fresh water
939 when temperatures were ≥ 30°C and DO level was 5 mg· L^{-1} (Kynard et al., 2009). The stationary
940 behaviour was interpreted as refuge seeking. However, in winter southern adult SNS use high (≥20
941 ppt) salinity in estuaries (Trested et al., 2011; Collins, M., unpbl. data).
942 Seasonal refuge is used by other sturgeons, with summer refuge being well-documented in
943 southern rivers for AS (Rogers et al., 1994). Similarly, there are cases where SNS moved to a
944 small refuge in summer before temperature increased and was limiting. However, the effect of
945 thermal and DO regime on movement to or selection of refugia by southern SNS is not clearly
946 understood. Recent evidence suggests southern SNS YOY may seek thermal refugia in summer
947 when temperature exceeds their temperature tolerance (Ziegeweid et al., 2008a, b). Thus, factors
948 responsible for refuge use of SNS may be specific to life stage as they are for GS.
949
950 **G. Effect of physical factors on habitat selection**
951 The effect of physical factors on habitat selection by SNS throughout the species range is poorly
952 studied. The best studied in both field and artificial streams are the physical factors (water depth,
953 water velocity, and substrate type) that affect spawning habitat selection of females (Buckley and
954 Kynard, 1985b; Kieffer and Kynard, 2012a; Kynard et al., 2010, 2012c), which is discussed in
955 detail in the section on spawning. The importance of physical factors, like temperature, water
956 depth, river geomorphology, etc. for selection of habitat are discussed in the appropriate life
957 history section dealing with spawning, foraging, wintering, migration, etc.
958
959 **H. Tolerance to contaminants and water quality**

960 Tolerance of sturgeons to contaminants is poorly understood, but recent studies suggest sturgeon
961 ELS are more sensitive to pollutants than ELS of most fishes. Dwyer et al. (2005) ranked SNS
962 among the two most sensitive species (of 17 listed species) to several chemical contaminants.
963 Further, juveniles and adults bio-accumulate dioxin and furans, and high levels that are potentially
964 damaging to SNS, although more studies are needed. Holcik (1989) cites the petrochemical
965 sensitivity to young sturgeons and maturing adults; Ruban (2005) cites many Russian studies that
966 evaluated the effects of pollutants on sturgeons. Connecticut River SNS free embryos and larvae
967 are sensitive to weathered coal tar (a byproduct of 19th Century gas lighting) that occupies patches
968 of the bottom in most Atlantic Coast Rivers (Kocan et al., 1996).
969 Jenkins et al. (1993) examined environmental tolerance to DO and salinity by SavR SNS and
970 found younger fish were more susceptible to low DO levels than older juveniles. Shortnose
971 Sturgeon juveniles older than 77 d experienced minimal mortality at nominal levels >2.5 mg·L^{-1};
972 while mortality at 2.0 mg·L^{-1} increased to 24−38%. In contrast, DO levels of 3.0 mg·L^{-1} resulted in
973 18−38% mortality of SNS <78 d old and mortality increased to 80% at 2.5mg·L^{-1}. Tolerance to
974 salinity also increased with age, so that larvae tolerated only 5 ppt, while yearlings tolerated 15
975 ppt, but not 30 ppt.
976 More rigorous testing using YOY SNS (77−134 d old) coupling temperature and DO factors
977 found a high degree of sensitivity even to low DO at low salinity (Campbell and Goodman, 2004).
978 This result emphases the problem for southern YOY SNS rearing in the freshwater: saltwater zone
979 when salt water begins to intrude more into fresh water (Jaeger et al., 2013). Fish exposed to low
980 DO levels (2.2−3.1 mg·L^{-1}) experienced a mortality rate of 96% within 4 h of exposure. Juveniles
981 (77 d) had an estimated median lethal concentration (LC_{50}) of 2.7 mg·L^{-1} at 25^{o}C; at temperatures
982 of 21.8−26.4^{o}C, and a LC_{50} of 2.2 mg·L^{-1} was found for YOY 104 and 134 d old. Juveniles (100 d)

exposed to 29°C were most sensitive to low DO, with a LC_{50} of 3.1 mg·L^{-1}.

Niklitschek (2001) observed poor survival of both SNS and AS at DO levels of 40% versus 70% saturation with the effect conditional on temperature. Bioenergetic and behavioural responses indicate that habitat for YOY (~30 to 200 d) becomes unavailable with less than 60% DO saturation (Secor and Niklitschek, 2001). This condition occurs in summer at temperatures of 22−27°C with DO of 4.3−4.7 mg·L^{-1}. Yearling SavR in the lab avoided water with a DO saturation of 40% (Niklitschek and Secor, 2010). Similarly, SavR YOY acclimated to 19.5 or 24.1ºC had critical thermal maxima of 33.7 or 35.1ºC, respectively, and a lethal thermal maxima of 34.8 and 36.1ºC (± 0.1ºC, respectively; Ziegeweid et al., 2008a).

Sublethal effects of low DO on SNS juveniles affects growth, metabolism, and foraging; further, a concurrent increase in water temperature amplifies the effects of low DO. Laboratory results indicated water temperatures of 20ºC and 40% DO saturation (i.e., 3.3 mg·L^{-1}), caused a 30% reduction in growth, a reduction in food consumption by about 28%, and a reduction in basal metabolism by about 20% (Niklitschek, 2001). While keeping DO saturation constant at 40% and increasing temperature to 27°C (corresponding to 2.9 mg·L^{-1} DO), growth was further reduced by 69%, consumption by 45%, and basal metabolism by 21% (Niklitschek, 2001).

Ontogenetic Migrations

Shortnose Sturgeon has a suite of migrations by each mobile life stage that is critical to a successful life history. The most complete understanding of migration or dispersal by all motile life stages (free embryos, larvae, juveniles, and adults) is for CR SNS, where decades of study in artificial streams and the river identified movements by life stage, and for some life stages, the

environmental factor(s) important for triggering movement (Kynard and Horgan, 202a; Kynard et al., 2012a, b, c, d, e; Kieffer and Kynard, 2012a). Spring upstream migration from wintering reaches by pre-spawning and non-spawning CR SNS is triggered by photoperiod and modulated by water temperature (Kieffer and Kynard, 2012a). In contrast, upstream non-spawning and pre-spawning staging migration by juveniles and adults in summer−fall is triggered by increased river discharge (Kynard, 1998; Kynard et al., 2012a, b). Downstream migration by adults during any season is not related to physical factors, like river discharge or water temperature and fish move on an individual schedule (Kynard et al., 2012a, e). The following section outlines behaviour and movements in detail by life stage.

A. Early life stages

Artificial stream studies found a latitudinal difference in the timing of downstream dispersal by ELS: northeastern populations disperse as larvae (Kynard and Horgan, 2002a; Kynard et al., 2012c) and southern populations begin dispersal as free embryos and continue as larvae (only SavR SNS studied; Parker and Kynard, 2005; Parker, 2007; Parker and Kynard, 2014). Savannah River SNS larvae continued a slow dispersal for months, much like GS larvae (Kynard and Parker, 2004). The southern dispersal likely moves larvae hundreds of kilometers downstream from the spawning reach. Connecticut River SNS free embryos (and likely free embryos in other northeastern and GOM populations) are photonegative and hide under rocks at the spawning site. Also, like in the CR, other northern SNS may begin dispersal as larvae (Taubert and Dadswell, 1980; Kynard and Horgan, 2002a; Kynard et al., 2010; Kynard et al., 2012c; Usvyatsov et al., 2012a).

Duration of dispersal by ELS is probably a local adaptation of SNS in each river. Duration of

CR SNS larval dispersal can be affected by water temperature ─ warmer temperature = longer dispersal duration (Parker, 2007). Studies on CR larvae found they typically disperse only a few days before stopping to forage (Kynard and Horgan, 2002a), whereas SavR SNS disperse for months (Parker and Kynard, 2014). The evolution of dispersal duration is likely related to several factors, such as density of benthic invertebrates on the dispersal route ─ for a short dispersal in northern rivers (where benthic invertebrate density is high) and a long slow dispersal in southern rivers (where invertebrate density is low; Parker and Kynard, 2014).

Migration by YOY is poorly documented except in the CR. The CR YOY in an artificial stream did not migrate downstream before wintering (Kynard and Horgan, 2002a; Parker and Kynard, 2014); thus, we assume this correctly reflects the situation for wild YOY. Information on YOY migration from other rivers is lacking.

B. Yearlings

Studies in an artificial stream found a major downstream migration by about 50% of the CR SNS yearlings, which is the downstream movement that distributes fish throughout the downstream concentration reaches (Kynard et al., 2012d, e). A downstream migration by yearlings to a lower river freshwater concentration reach or to a freshwater: saltwater reach may be typical of SNS throughout the range, but data are lacking from most rivers. Field data from other northern and southern rivers on the timing of the arrival of yearlings at the freshwater: saltwater zone support the downstream migration timing of CR yearlings found in the artificial stream (Hall et al., 1991; Dovel et al., 1992; Collins et al., 2002). In summary, after overwintering in fresh water and developing salinity tolerance, the downstream migration of yearlings to the freshwater: saltwater reach may be a common migration pattern throughout the range.

C. Yr-2+ juveniles and adults

Throughout the species range, yr-2−3 juveniles remain in the natal river-estuary (Dadswell et al., 1984), but study is needed on telemetered juveniles of different ages to understand their movements in better detail. Juveniles and adults use the same riverine and estuarine concentration reaches. Also, some fish return (home) to the same reach annually, while other fish change and move upstream or downstream, nearer or farther away from the spawning reach depending on their stage of reproductive maturity (Bay of Fundy, GOM, and northeastern rivers – Dadswell, 1979; Buckley and Kynard, 1985a; Dovel et al., 1992; Kieffer and Kynard, 1993; Kynard et al., 2000; Fernandes, 2008; Kynard et al., 2012a).

In the CR, most pre-spawning females have a two-step migration to spawn (Kynard, 1997; Bemis and Kynard, 1997). The first step is an upstream pre-spawning staging migration (Northcote, 1978): when females migrate upstream past two long rapids in the summer–fall, and then, spend the winter at the most upstream part of the upstream concentration reach (Deerfield) just 10 rkm downstream from the spawning reach at Montague (Kynard et al., 2012a). The second step is the spawning migration: in spring, pre-spawning females and males leave the wintering reach at Deerfield and migrate only 10 rkm to spawn at Montague (Kieffer and Kynard, 2012a). Pre-spawning DelR females may also have this migration style because they spend the winter just downstream from the spawning reach (O'Herron et al., 1993). Most pre-spawning CR males (and a few small females) in the downstream segment have a one-step pre-spawning migration in spring moving as far as 150 rkm upstream from wintering reaches in the lower-river to attempt to spawn at Montague (Kynard et al., 2012a).

The different seasonal migration strategies of CR males and females is likely related to

migration distance, migration difficulty due to the long rapids, and energetic resources available to each sex after 5 mo of wintering (Kynard et al., 2012a, e). For large females, the best strategy is a summer–fall upstream pre-spawning staging migration to Deerfield during high river flows, when they are foraging, in good physical condition, and water temperatures are warm instead of in spring, when river discharge is just as great, if not greater, fish are in poor condition, and it is cold (6−7°C; Kynard et al., 2012a, b, e). The difficulty of migrating upstream through CR rapids in spring is illustrated by the inability of all six radio-tagged SNS adults tracked in spring 1983 to swim past the Enfield Rapids (Buckley and Kynard, 1983b). Large CR SNS females have a pre-spawning staging migration to Deerfield in summer-fall, overwinter there, and then in spring, migrate only 10 km upstream to spawn (Kynard et al., 2012a; Kieffer and Kynard, 2012a). The two-step migration pattern (pre-spawning staging + short spawning migration) may be common for sturgeon species with 1) a difficult but short total migration distance (like CR SNS), and 2) a long distance migration like the 1678 rkm migration by Yangtze River Chinese Sturgeon, *A. sinensis* (Wang et al., 2012). Fall-spawning AS may also have a two-step pattern (Post, W., SC Dep. Nat. Resour., Charleston, SC, unpbl. data).

Interesting, a one-step spawning migration by pre-spawning SNS occurs in the Bay of Fundy, GOM rivers, and in the HudR (Squires, T. et al., 1993; Kynard, 1997; Bain, 1997; Usvyatsov et al., 2012a). This pattern also occurs in all southern rivers yet studied (Hall et al., 1991; Collins and Smith, 1993; Moser and Ross, 1995; Rogers and Weber, 1995; Devries and Peterson, 2006). During a one-step migration, females migrate directly to spawn in late-winter or spring, depending on latitude. A one-step migration by a pre-spawning female also occurred in the mid-Atlantic PotR (Kynard et al., 2009), which was like SNS in southern rivers that swim the entire distance to spawn in late-winter or early-spring (Kynard, 1997). Departure of a significant

proportion of late-stage females from summering foraging in the PenobR, to wintering sites in the KenR complex in the fall where they will spawn in spring appears analogous to the two-step spawning migration of late-stage CR females (Kynard, 1997; Dionne, 2010). Other late-stage adults in the PenobR overwinter and in spring, migrate to the KenR to spawn, perhaps analogous to a one-step migration, like that of most CR males and small females (Dionne, 2010; Kieffer and Kynard, 2012a; Kynard et al., 2012a). Thus, adults are flexible for spawning migration likely depending on their age or size, individual reproductive characteristics, and distance from the spawning site.

D. Straying from natal rivers

Coastal migrations by adult SNS that leave natal rivers and migrate along the coast is well documented throughout the species range (Dadswell et al., 1984). Kynard (1997) reported most coastal migrants occurred in the northern part of the range, where populations are large, suggesting the presence of a density-dependent regulating mechanism in SNS river populations. Cultured CR SNS have a size-dominated social feeding hierarchy, which if this occurs in wild SNS populations, could serve as the social basis for density regulation (Kynard and Horgan, 2002a).

As discussed previously, adult SNS have been captured or their telemetry tags detected as they migrate in the near-shore zone along the coast and even when they enter non-natal rivers (Dadswell et al., 1984; Kynard, 1997; Savoy, 2004; Fernandes, 2008; Dionne, 2010; Zydlewski et al., 2011; Kieffer, M., unpbl. data; Wippelhauser et al., 2015). Coastal migrations that result in spawning of adults in a non-natal river would create gene flow among river populations and a metapopulation, but the actual spawning of emigrant adults in a non-natal river is undocumented. Recent telemetry studies of SNS movements in the GOM found adults moved among several large

and small rivers in a complex pattern using river, coastal, and estuarine habitats (Dionne, 2010; Fernandes et al., 2010; Zydlewski et al., 2011; Wippelhauser et al., 2015). Inter-river movement of SNS may be a feature of local geography, where larger river systems occur in relatively close proximity, with numerous smaller systems residing in between (Dionne, 2010; Zydlewski et al., 2011). Such movement patterns are often seasonally constrained and directed, with migratory individuals commonly returning to the same river at the same season in different years (Fernandes, 2008; Dionne, 2010; Kieffer, M., unpbl. data).

Movements of GOM and southern SNS among rivers seems similar to the complex movements of CR SNS among different concentration reaches within the one large river system where three major foraging–wintering concentration reaches exist (Connecticut, Agawam, and Deerfield; Buckley and Kynard, 1985a; Kynard et al., 2012a, b, e).

Analysis of range-wide population genetics also suggests a significant historical degree of mixing among southern rivers (King et al., 2008, 2014). However, the similarities in alleles among southern populations could have occurred when population abundance was greater. The increased incidence of coastal movements and metapopulations in both GOM and southern rivers suggest, if suitable riverine spawning and early rearing habitat are present, the long-term prognosis for coastal migrants throughout the range is to colonize rivers where populations have been extirpated.

E. Inter-basin Translocations

Transfer of wild SNS juveniles or adults between basins has not been undertaken for any restoration effort. However, some of almost 100,000 cultured, mostly-unmarked groups of SavR juveniles stocked in the Savannah River during the 1980s and 1990s has resulted in a few of the

1142 marked fish moving into many southern rivers (Smith et al., 1995). Is this an example of abnormal
1143 movements by stocked fish due to a lack of imprinting by ELS, natural movements, or a
1144 combination? Although natural movements of SNS between southern rivers occurs (Collins, M.,
1145 unpbl. data), the massive number of stocked unmarked fish make conclusions difficult regarding
1146 movements among rivers as long as these stocked fish are alive.
1147 Wandering of cultured HudR juvenile AS stocked into non-natal tributaries of Chesapeake
1148 Bay (Secor et al., 2002) suggests that wandering is typical of cultured juveniles stocked into a non-
1149 natal river without having been imprinted as ELS to water from the natal river. Sequential
1150 imprinting during early life to the natal river is likely important for a successful life history of
1151 SNS, and probably, for all sturgeons (Kynard et al., 2012a).
1152 Shortnose Sturgeon movement suggests evolution of life history movements where each fish
1153 moves to a particular concentration reach at a certain time of life, i.e., each fish is on an individual
1154 movement schedule related to its age and reproductive condition (Kynard et al., 2012c, e).
1155 Abnormal movements of pre-spawning CR females passed upstream of Holyoke Dam was
1156 interpreted as abnormal behaviour that resulted from Holyoke Dam blocking successful upstream
1157 migration and exposure of downstream segment juveniles and adults to water in the upstream
1158 concentration reach (Kynard et al., 2012a). Impeding natural movements and translocating fish
1159 into non-natal rivers likely creates abnormal movements and a lower fitness for these individuals.
1160

1161 **F. Distance traveled and rate of movement**

1162 The longest distance typically traveled downstream by dispersing SNS larvae in the CR is <20 km
1163 in <7 d (Taubert and Dadswell, 1980; Kynard and Horgan, 2002a). Although the distance traveled
1164 is not known for SavR free embryos and larvae, artificial stream observations suggest fish travel

hundreds of kilometers during the many weeks of dispersal (Parker and Kynard, 2014).

Most telemetry tracking to determine movement rates has been on pre-spawning adults in northeastern and southern rivers. Movement rate of pre-spawning CR males was 0.7−10 rkm·d^{-1} ground speed in April and the mean maximum ground speed during 24 active movement segments by pre-spawning males was 4.5 rkm·d^{-1} (range, 1.0–10.0 rkm·d^{-1}; Kieffer and Kynard, 2012a). Pre-spawning CR females left wintering reaches after males and moved to spawning grounds at a rate similar to the slowest males (Kieffer and Kynard, 2012a). Pre-spawning adults in the CapFR moved upstream at 0.78−1.07 BL·s^{-1}, an average ground speed of 11.5−27.0 rkm·d^{-1} (Moser and Ross, 1995). Pre-spawning SavR adults moved upriver in late-January−mid-March, traveling at an average speed of up to 50 rkm·d^{-1} (Collins and Smith, 1993). Hall et al. (1991) also reported upriver migration by pre-spawning SavR adults during February and March at speeds of 1−33 rkm·d^{-1}.

Movement speed depends on reproductive stage and is also affected by riverine factors, temperature and discharge. Non-spawning CR adults moving upstream between concentration reaches moved a mean of 16 rkm·d^{-1} (SD = 6 rkm), while CR adults moving downstream between concentration reaches moved at a lower mean rate of 10.5 rkm·d^{-1} (SD = 15 rkm; Buckley and Kynard, 1985a). Interestingly, post-spawned CR adults traveled downstream at about the same speed as upstream migrants (Kynard et al., 2012b). River temperature did not affect pre-spawning migration duration of CR adults, but high discharge was significantly related to longer and slower migrations. Ground speed of upstream migrant pre-spawning adults was slower with increasing river temperature and increasing discharge (Kieffer and Kynard, 2012a).

Adult CapFR SNS whose pre-spawning upstream migration was interrupted in the CapFR moved downstream at the rate of 8.5−36 rkm·d^{-1} (Moser and Ross, 1995). Mean daily upstream

movement rate of DelR juveniles (391−483 mm FL) was 4.1−7.3 rkm and the maximum daily movement was 14−40 rkm (Brundage and O'Herron, 2009).

Movement rate of adults in GOM estuaries was 8.1−34 cm·s $^{-1}$ (0.07−0.37 BL· s^{-1}) and movement often occurred with a rising tide (McCleave et al., 1977). Marine migration of SNS between GOM rivers can cover a distance of >140 km in as little as 6 d (average, 14 d), suggesting a conservative directed swimming speed of 23.3 km·d^{-1} (average, 10 km·d^{-1}) in marine and estuarine habitats (Dionne, 2010; Kieffer, M, unpbl. data; Dionne, P., Univ. Maine, Orono, unpbl. data).

G. Habitat used during migration

Shortnose Sturgeon larvae in GOM and northeastern rivers were captured in the river channel near the bottom. Drift nets set in the CR at various water depths and locations across the river captured all dispersing larvae within 1 m of the bottom in the channel (Taubert and Dadswell, 1980). Kieffer and Kynard (1996, 2012a) and Kynard et al. (2012b) found similar results in the CR and the MR. Bath et al. (1981) captured HudR larvae near the bottom of the channel. So, northern larvae are in the channel within 1 m of the bottom.

During upstream or downstream movements by telemetry-tagged CR or MR adults, most were in the channel. Kynard et al. (2012b) found CR adults moved downstream in the channel, and Kieffer and Kynard (2012a) found upstream migrant pre-spawning CR used the channel. Upstream migrant MR adults are similar to CR adults (Kieffer, M., unpbl. data). During upstream or downstream movements, all life stages appear to follow the channel, the habitat with the greatest predictability for the most direct route upstream or downstream.

Reproduction, Spawning, Early Life History

A. Imprinting and homing to spawn

Many years of monitoring CR SNS migrating to the one spawning grounds found zero juveniles or immature adults accompany the spawning cohort (Kieffer and Kynard, 2012a). Thus, the year when adults first return to spawn is their first time to return to the natal spawning reach since they left as free embryos or larvae. This suggests imprinting begins with free embryo and larval life stages at the spawning reach and is an adaptation to guide a virgin adult back to the spawning reach (Kynard et al., 2012a).

B. Spawning reach homing

In all rivers where spawning reaches have been monitored for SNS use for several years, adults return (home) to the same reach with 100% fidelity. Buckley and Kynard (1985a) found this situation for CR SNS adults and later studies during 18 yr found adults homed to the same 3 km spawning reach where bottom velocities and substrate size were the physical factors that affected spawning timing and determined use of a specific spawning location (Kieffer and Kynard, 2012a). Not only did CR adults return to the same reach, but they spawned annually in the same small sites. Multi-year homing to the same spawning reach has also been documented in the MR (Kieffer and Kynard, 1996; Kieffer, M., unpbl. data), the AndR (Squires et al., 1993), and the DelR (O'Herron et al., 1993; Brundage, H., unpbl data). Unlike sturgeon species that spawn at multiple reaches located at different distances from the river mouth (Parsley and Beckman, 1994; Schaffter, 1997; Kynard et al., 2002; Ruban, 2005; Zhang et al., 2008; Suciu, R., Danube Delta Res. Inst., Tulcea, RO, unpbl. data), SNS in all rivers yet studied spawn at one reach, the most upstream reach used during their life history.

1234

1235 **C. Spawning interval**

1236 The spawning interval is shorter for males than for females throughout the range (Dadswell et al.,
1237 1984). Recent long-term studies on CR SNS determined the spawning interval for upstream
1238 segment adults was 1–5 yr (mean, 1.4 yr) for males and 2–10 yr (mean, 4.5 yr) for females (Kieffer
1239 and Kynard, 2012a). Further, all MR males (N = 5) tracked for 2–5 yr spawned annually (Kieffer
1240 and Kynard, 1996). For mid-Atlantic SNS, one PotR female returned to spawn after only 3 yr
1241 (Kynard et al., 2009; Mangold, M., USFWS, Annapolis, MD, unpbl. data), which is the normal
1242 spawning interval for southern females in SC and GA, where most males spawn annually
1243 (Peterson, D., unpbl. data).

1244

1245 **D. Sex ratio during spawning**

1246 Pre-spawning males always outnumber females on SNS spawning grounds (Dadswell et al., 1984).
1247 However, quantitative information on annual sex ratios at a spawning ground to support this
1248 statement is mostly lacking. Long-term (17 yr) studies on CR adults quantified the annual variation
1249 for sex ratios as: mean male: female sex ratio = 11.2:1 in years when spawning succeeded and =
1250 9.9:1 in years when spawning failed (Kieffer and Kynard, 2012a). Thus, sex ratio of pre-spawning
1251 adults at spawning grounds gives no clue as to spawning success or failure of annual spawning.

1252

1253 **E. Spawning timing and environmental cues**

1254 Although water temperatures when spawning occurs has been noted by many researchers
1255 (Dadswell et al., 1984; Buckley and Kynard, 1985b; Kieffer and Kynard, 1996; Cooke and Leach,
1256 2004, et al., 2002; Environ. Res. and Consult, Inc, 2008; Usvyatsov et al., 2012a), only in the CR
1257 have environmental factors correlated with SNS spawning timing been studied annually for many

consecutive years (17 yr). Male CR SNS arrive at the spawning reach prior to females and successful female spawners typically spend only 6 d on the spawning grounds (Kieffer and Kynard, 2012a). Most importantly, spawning of CR females only occurred when three spawning suitability windows were simultaneously open: (1) day length = 13.9−14.9 h (27 April–22 May), (2) mean daily water temperature = 6.7–15.9 °C, and (3) mean daily river discharge = 121–901 $m^3 \cdot s^{-1}$. The annual spawning period for CR females was short (3–17 d), which may be typical when only a few females are present. Connecticut River females typically moved downstream from the spawning reach within 24 h after spawning (Kieffer and Kynard, 2012a).

Wild CR SNS females observed spawning in an artificial stream began spawning within 36–81 h after introduction into the stream and access to ripe males. This result shows females can quickly spawn when the photoperiod and temperature spawning windows are open and spawning habitat and ripe males are present (Kynard et al., 2010, 2012c). Like the spawning timing for other north temperate teleost fishes (Baggerman, 1980), photoperiod is the dominant environmental factor determining spawning timing of CR SNS. Further, groups of pre-spawning CR females held during winter in cold (ambient CR river water 2-5°C) and groups of females held in warm water (7−9 ºC), that were combined in spring and introduced into an artificial stream began spawning on the same date (Kynard et al., 2012c). This is further evidence that photoperiod, not water temperature, is the main environmental factor controlling spawning readiness of CR SNS females. Whether this is the situation for southern SNS has yet to be studied.

F. Spawning style

Shortnose Sturgeon has a long-duration spawning style. Females in an artificial stream spawned for 20−30 h for an average-size female, but spawning duration was dependent on female size

(longer spawning time for females with the most eggs; Kynard et al., 2012c). Females ovulated and spawned batches of several hundred eggs every 15−20 min (3–4 spawning bouts·h^{-1}), did not stop once spawning began, and placed small batches of eggs (several hundred) at discrete bottom sites. In the artificial stream, females had a spatial bias and repeatedly spawned at the same location, a bias that was also found during tracking of wild spawning CR SNS females (Kieffer and Kynard, 2012a).

Males and females mated with multiple mates in the artificial spawning stream, suggesting a polygamous mating style for wild fish with no mate bonding (Kynard et al., 2012c). Mate bonding suggested by Dadswell (1979) is unlikely because of the vastly different maturity schedules of males and females. Multiple-year tracking of wild CR adults (Kieffer and Kynard, 2012a) support observations in the artificial stream for polygamous mating

Mating success of males in the artificial stream was not related to body size (Kynard et al. 2010, 2012c). Observations on mating pairs suggest male success was related to reproductive drive, competitive skill, and skill at guiding females. Field studies also identified dominant and subordinate males during spawning (Kieffer and Kynard, 2012a).

The SNS mating system includes sneaker males, when smaller males obtain a fertilization of some eggs via covert movements while older larger males are spawning. In the artificial spawning stream, sneaker males swam quickly to a spawning pair and squirted a jet of sperm near the female's posterior when the larger spawning male vibrated and released sperm (Kynard et al., 2012c).

G. Spawning site location

1303 The lack of salinity tolerance by SNS ELS could be one primary factor determining the evolution
1304 of females selecting a spawning reach that is far upstream from salt water. All studies indicate that
1305 YOY require ≥300 d to develop a tolerance to moderate salinity (5–10 ppt) that is needed to use an
1306 estuary (Jenkins et al., 1993). Thus, young life stages of SNS are adapted to rear only in fresh
1307 water. Ionic regulation of salt by SNS juveniles was studied by Krayushkina (1998).
1308 Although suitable spawning habitat (rocky bottom and moderate bottom water velocities)
1309 may exist at a river rapid, this does not mean that SNS will use the place as a spawning reach, if
1310 imprinting by ELS has not occurred to water in the reach. In the CR, abundant spawning habitat
1311 exists at two rapids far downstream from the third rapids at rkm 193−194 (Montague), where
1312 upstream segment adults and displaced downstream segment adults spawn (Kynard et al., 2012a, b;
1313 Kieffer and Kynard, 2012a). Thus, spawning habitat availability is only relevant at the geographic
1314 spawning reach used by females.
1315 In all populations yet studied, the spawning site is the most upstream river reach used by
1316 SNS, although a rare adult may forage upstream of the site (Kynard, 1997; Kieffer, M., unpbl.
1317 data). This situation seems the case in all rivers throughout the range (north to south): SJohnR –
1318 Litvak, M., unpbl. data; MR – Kieffer and Kynard, 1996; Kieffer, M., unpbl. data; CR –Taubert,
1319 1980a; Kynard, 1997, et al., 2012e; HudR − Dovel et al., 1992; Bain, 1997; DelR − O'Herron et
1320 al., 1993; PotR – Kynard et al., 2009; CapFR – Moser and Ross, 1995; SavR – Hall et al., 1991
1321 and Collins and Smith, 1993; CongR – Collins et al., 2003; GPeeDR – Collins, M., unpbl. data;
1322 AltR− Rogers and Weber, 1994a, b, 1995.
1323 Spawning has been observed in several rivers in the tailrace just downstream of hydropower
1324 dams (Cooke and Leach, 2004; Squires et al., 1993; Kieffer and Kynard, 2012a) and also, at
1325 natural rapids (O'Herron et al., 1993; Kieffer and Kynard, 1996, 2012a; Usvyatsov et al., 2012a).

All sites typically have a rough bottom (usually, cobble-gravel rocks or hard clay bits) and moderate bottom velocities (maximum, about 100 $cm \cdot s^{-1}$; see Kieffer and Kynard, 2012a and Kynard et al., 2012c).

When access to the natural spawning site is blocked by a dam, adults in some rivers spawn in the tailrace of the hydropower station (Cooke and Leach, 2002; et al., 2002). In the CR, pre-spawning downstream segment females that annually migrate upstream to Holyoke Dam in spring were believed by Buckley and Kynard (1985b) and Root (2001) to spawn there. However recent studies found only a rare female spawns at Holyoke (Kynard et al., 2012b). Spawning at Holyoke does not occur even though studies found suitable spawning habitat is abundant in the tailrace and in the rapids downstream of the dam (Buckley and Kynard, 1985b; Kynard, 1999; et al., 2012b). Thus, downstream segment CR females blocked by Holyoke Dam abort spawning rather than spawn at the dam, which is located 52–53 rkm downstream from the Rock Dam reach in Montague, the historical spawning reach. Further, downstream segment adults that are displaced upstream of the dam spawn at Montague with upstream segment adults (Kynard and Kieffer, 2012a, b; Kieffer and Kynard, 2012a; unpbl. data). The difference between SNS populations for females that spawn below a dam blocking migration, suggests females in some SNS populations are more genetically hard-wired to home to their historical spawning reach than females in other populations.

An alternative hypothesis for the lack of spawning by downstream segment females at Holyoke Dam could be due to the absence of a river parameter cue (possibly, a water chemistry factor like pH or Ca++ ion) that is insufficient to trigger spawning at Holyoke but is sufficient to trigger spawning upstream at Montague (Sulak, K., pers. comm.). The existing water quality information does not support this hypothesis: 1) pH is 6.8–7 and alkalinity levels (as $CaCO^3$) are

1349 20 $Mg \cdot L^{-1}$ in May (when spawning occurs) at both Holyoke and Montague (MAWPC, 1978, 1980;
1350 Kynard, B., unpbl. data). Further, spawning at the Holyoke reach of rapids would make two
1351 widely-separated spawning reaches, which is not consistent with the pattern of only one spawning
1352 site at about rkm 200 found in all northeastern SNS populations (Kynard, 1997; Kynard et al.,
1353 2012a, b, e).

1354 The size of spawning grounds has only been estimated for the Montague reach in the CR,
1355 where spawning in the Cabot Station tailrace site is 2.7 ha and spawning at the natural Rock Dam
1356 site is 0.3 ha (Kieffer and Kynard, 2012a). The small spawning reaches used by CR females are
1357 likely a reflection of the few females present (tens, not hundreds) and the size of spawning sites
1358 would probably be much larger if (when?) pre-spawning downstream segment females blocked by
1359 Holyoke Dam are passed upstream of Holyoke Dam and have access to the Montague spawning
1360 reach. Because egg density (number $eggs \cdot m^2$) greatly affects survival to the larval stage (Fig. 4;
1361 Kynard et al., 2010, 2012c), it seems likely that size of the spawning reach will be directly
1362 proportional to the number of females present.

1363 Use of the two Montague spawning sites (Rock Dam versus the Cabot Station tailrace) by
1364 females is dependent on river regulation by Turners Falls Dam. Although adults initially go to the
1365 Rock Dam, as the dam gains control of river flow and flow to Rock Dam decreases and bottom
1366 velocity falls below a SNS female's innate velocity preference, females (and males) leave Rock
1367 Dam, move 1 rkm downstream and attempt to spawn in the Cabot Station tailrace, the only source
1368 of moderate velocity. River regulation caused SNS to depart the low natural flow to Rock Dam in
1369 more than ½ of the 17 years spawning was monitored (Kieffer and Kynard, unpubl. data). During
1370 hearings to relicense Cabot Station, a minimum of 2400 cfs for the reach of river with SNS

spawning is being requested from mid-April to June (during pre-spawning period of adults through the rearing period of ELS (Kynard, B., unpbl. data).

Shortnose Sturgeon females can spawn in hydroelectric dam tailraces, like a rare female at Holyoke Dam and many females at Cabot Station on the CR, and also, in the tailrace of other dams, like Pinopolis Dam (Cooke and Leach, 2004). However, water flow (and bottom velocity) from hydroelectric turbines varies greatly through time and space and it seems there is a great chance these ELS can be swept away during the several weeks needed to rear embryos and free embryos. Within the Cabot Station tailrace, specific spawning locations appear to vary from year to year due to different turbine generation regimes (Kieffer and Kynard, 2012a), which change according to operational demand. Further, in response to generation variation, the spawning of females in the tailrace is not continuous through time. Females often leave the tailrace spewing unfertilized eggs before returning to the tailrace to resume spawning, likely under flow conditions more favorable to spawning (Kieffer and Kynard, 2012a).

H. Spawning microhabitat

Microhabitat has been studied best in the CR using telemetered adults to identify when spawning occurs. Female CR SNS spawned in water depths of 1–5 m, with most spawning in water 1.5–1.9 m deep (Kieffer and Kynard, 2012a; Fig. 5a). Also, females spawned in moderate water velocities (mean, 70 $cm \cdot s^{-1}$; range, 20–130 $cm \cdot s^{-1}$) with peaks at 20–50 and 70–120 $cm \cdot s^{-1}$ (Fig. 5b). The dominant substrate was cobble (rubble) 65–256 mm diameter; subdominant in abundance was pebble (64–16 mm) and gravel (16–2 mm diameter; Fig. 5b).

Characterization of spawning substrate used in three rivers (CR, MR, AndR) found some minor differences, but a similar substrate composition (mixture of rubble and smaller rocks) was

always present (Kynard et al., 2012b). Southern SNS in the CoopR spawn over a clay marl substrate (Duncan et al., 2004), but no details about the bottom (abundance, size, or composition of clay pieces) were recorded. Connecticut River SNS females in an artificial spawning stream spawned for 7 yr over a rubble−pebble substrate with the following composition and size range: small pebble (16−32.5 mm diameter) = 6.6%, large pebble (32.6−64.4 mm) = 52.5%, and rubble (64.5−256 mm) = 40.9%.

Water depth is not an important factor in selection of spawning site by wild CR SNS females spawning in the river (Kieffer and Kynard, 2012a). Also, in the artificial spawning stream, CR females spawned for 7 yr in water only 60 cm deep.

The mean water velocity in the artificial stream at 0.6 m depth was 48 $cm \cdot s^{-1}$ (range, 17–126 $cm \cdot s^{-1}$). This velocity is within the acceptable range for females (Kieffer and Kynard, 2012a; Kynard et al., 2012c).

Successful spawning of SNS has been observed in many northern rivers, but the chemistry of the water during spawning has not been studied. Shortnose Sturgeon with free access to river length spawn at about 200 rkm or greater in a wide range of rivers from Canada to Georgia (Kynard, 1997). This indicates the species has a wide tolerance to water chemistry factors like pH, CA++ that can affect sperm and egg function (Detlaff et al., 1993). Thus, females may select spawning sites based on other environmental factors, like bottom velocity and substrate type, which seem critically important to egg and free embryo survival (Kieffer and Kynard, 2012a). While this appears to be the case in the CR (see Spawning Site Selection Section), the importance of chemistry to spawning site selection by SNS in other rivers has not been studied.

I. Spawning behaviour

In observations made in the artificial spawning stream, males began courtship by nuzzling a female's vent and rubbing their head along her body (Kynard et al., 2012c). Possibly, males emit a pheromone that stimulates females because males often rubbed their anal area on a female's head.

Spawning by SNS has only been observed closely in the artificial spawning stream (Kynard et al., 2010, 2012c). Adults did not emit a call during courtship or spawning; instead, the synchronization cue for gamete release was a physical stimulus of a male quivering and vibrating strongly alongside the female. Males detect pheromones from females (Kynard and Horgan, 2002b), which explains why pre-spawning females minimize swimming after reaching the spawning reach (Kieffer and Kynard, 2012a). Males are attracted to females by their pheromone, so males are always present when a female begins to ovulate eggs.

In the artificial stream, several males were always following each pre-spawning female, and all were swimming loops around the oval artificial stream. Once spawning began, males kept following the female very close and were always in position to maneuver into position to lie with the female and spawn when the female briefly stopped swimming. Field studies also found several tagged males accompany each tagged female (Buckley and Kynard, 1985b; Kieffer and Kynard, 2012a; Kynard et al., 2012b).

During spawning, behavior of females and males were coordinated where the female led the behavioural series and males followed in stereotypical fashion. Typical behaviour during spawning in the artificial stream was all females swimming separately around the large artificial stream against the current, with each female closely followed (within 1.0−2.0 m) by several (3−5) chaser males. This ratio of females to males in the spawning group is the same ratio as found for captured wild adults in a pre-spawning or spawning group (Buckley and Kynard, 1985b; Kieffer and Kynard, 2012a; Kynard et al., 2012b). The exception to swimming loops was large females, who

1440 stayed immobile near their preferred spawning site in the artificial stream. They periodically
1441 moved to spawn, and then, returned to their resting spot. Spawning occurred when a female paused
1442 swimming and rested immobile for a few seconds on the substrate. Then, one chaser male quickly
1443 sidled alongside her body (head to head), and vibrated strongly beating his tail against her body.
1444 This vibration seemed to be the stimulus for a simultaneous release of male and female gametes, as
1445 sperm and eggs were visibly observed being released during tail beating (Kynard et al., 2010).
1446 After the typical 5 sec spawning pause, the female resumed swimming against the current with
1447 chaser males following.

1448 Some males were much better than others at guiding females to pause and spawn and some
1449 males obtained many more spawning events than others, data showing an unequal fitness of males
1450 (Kynard et al., 2010, 2012c). Further, some females did not spawn in the artificial stream, a
1451 situation that also occurs among wild females (Kieffer and Kynard, 2012a). This information on
1452 sturgeons is ignored in conservation culture and stocking of fry for restoration.

1453

1454 **J. Annual spawning success**

1455 Spawning can fail in any year because 1) pre-spawning adults fail to migrate from wintering
1456 grounds to spawn (pre-spawning migration failure) or 2) because environmental conditions at the
1457 spawning site never satisfy a female's habitat preferences when the three spawning windows are
1458 open (Kieffer and Kynard, 2012a). Pre-spawning migration failure is likely related to reduced
1459 energetic resources of wintering fish caused by inadequate summer-fall foraging and a demanding
1460 energetic environment (high temperatures, low river flows, or both) during the previous summer-
1461 fall foraging season or on high flows (and high energetic demand) during wintering (Kieffer and
1462 Kynard, 2012a). These results suggest the strategy of adults is to abort spawning if low energetic

resources could reduce the chance to survive and spawn in a later year. Year-class strength of HudR SNS is related to river flow in the fall months preceding spawning, with high flows in fall resulting in larger year classes (Woodland and Secor, 2007).

If females carrying a clutch of eggs do not spawn due to any factor, do they reabsorb eggs and return to spawn earlier than females that spawned? Experiments that held pre-spawning female SNS and did not allow them to spawn found some held dead eggs for months without adsorption, while others ejected dead eggs within a few weeks. Most importantly, telemetered pre-spawning wild CR females that failed to spawn in the river during yr x did not return to spawn earlier than females that spawned in yr x and had to develop a new clutch of eggs (Kieffer and Kynard, 2012a). Thus, whether wild females that fail to spawn aborted or absorbed their dead eggs, the female does not seem to gain a benefit that allows them to develop a new clutch of eggs earlier than females that spawned.

The proximate environmental factor responsible for repeated annual spawning failure in the CR was river discharge, which determines the critical proximate factor for spawning — bottom velocity (Kieffer and Kynard, 2012a; Kynard et al., 2012c). Discharge is highly regulated by hydropower dams in the CR and extremes of low or high regulated discharge caused repeated spawning failures at the Rock Dam natural spawning reach in Montague (Kieffer and Kynard, 2012a). In the artificial spawning channel, fast velocity could be switched from one side of the channel to the other and by switching only velocity from one side to the other side, females could be made to change sides to spawn in the fastest available velocity (Kynard, et al., 2012c, unpbl. data).

K. Early life stages

1486 Dadswell et al. (1984) described the earliest life stage (egg = embryo) as brown-blackish, 3–3.2
1487 mm diameter for mature eggs, with little change in diameter after fertilization. At 8–12 ºC, eggs
1488 hatch after about 13 d or 136–143 degree-days. Length at hatching is 7.3–11.3 mm (Taubert,
1489 1980b; Buckley and Kynard, 1981).

1490 Snyder (1988) described the morphology and development of the free embryo life stage
1491 (yolk-sac larva of Shortnose Sturgeon Status Review Team, 2010) and larvae. Further, Richmond
1492 and Kynard (1995) made electron-micrographs of free embryos and larvae showing development
1493 of external sensory characters and the rapid development of the olfactory system (which is needed
1494 for imprinting to water). Hilton and Bemis (2012) illustrated the early stages of whole CR SNS
1495 specimens, as well as cleared and stained specimens showing the early development of the bony
1496 skeleton. As with Chinese Sturgeon, dorsal skeleton features develop before ventral features,
1497 suggesting a strong dorsal structure is needed to protect young fish from predators (Ma, J, South
1498 China Sea Res. Instit., Shanghai, China, unpbl. data).

1499 Egg fertilization observed in the artificial spawning stream found a SNS male's milt was
1500 released as he lay beside the female (Kynard et al., 2010, 2012c). After release, distribution of the
1501 low density milt and the heavy density eggs separate in the current allowing only an estimated
1502 5−10 sec for fertilization to succeed or fail. After several minutes of exposure to water, eggs are
1503 sticky and attach to any solid substrate (rocks, wood, leaves, plastic, etc.; Kynard, B. and E.
1504 Parker, unpbl. data).

1505 Spawning habitat is also rearing habitat for two ELS life stages: eggs and free embryos
1506 (Kynard and Horgan, 2002a). Because the female's body is resting immobile on the bottom during
1507 spawning, many eggs in the artificial spawning channel went directly into rocky substrate or
1508 drifted just a few meters downstream (Kynard et al., 2010; Kynard et al., 2012c). Egg drift in the

artificial stream totally ceased within 2 d after spawning ceased. A few free embryos and larvae of CR SNS drift tens of kilometers (Taubert and Dadswell, 1980), but drifting damages these life stages and likely kills them (Kieffer and Kynard, 2012a).

Free embryo behaviour is best studied on CR and SavR SNS. Artificial stream studies found CR free embryos are strongly photonegative and should hide under cover at a spawning site (Richmond and Kynard, 1995; Kynard and Horgan, 2002a). A few free embryos drift daily, mostly at night; however, this is not dispersal (Kynard et al., 2012c). However, SavR free embryos did not hide at the spawning site, but instead, dispersed slowly downstream (Parker, 2007; Parker and Kynard, 2014). This difference between CR and SavR free embryos, suggests a latitudinal difference in behaviour and dispersal initiation time between northeastern and southern SNS. The difference may be related to a lack of predators on CR SNS eggs and free embryos (Kynard and Horgan, 2002a); thus, CR SNS free embryos can remain under rocks to develop into larvae before dispersing. Perhaps, predation is greater on eggs and free embryos in southern rivers, so they disperse as free embryos.

Local adaptation for dispersal timing and duration seems the rule for SNS ELS. Connecticut River SNS larvae are strongly photopositive (Richmond and Kynard, 1995) and disperse only a few days (Kynard and Horgan, 2002a), whereas in the SavR, both free embryos and larvae disperse. The mostly nocturnal dispersal is short (few days) in the CR and long (months) in the SavR (Kynard and Horgan, 2002a; Parker and Kynard, 2014).

Survival of ELS and sources of mortality are poorly studied in the wild. Kynard and Horgan (2002a) examined stomachs of predators at the SNS Montague spawning site and found almost no fish predation on ELS. This may be due to the scarcity of females and few eggs. Survival of CR SNS ELS in the artificial stream, which exposed fish to physical conditions like a natural stream

and invertebrate predators, but no predatory fish, was inversely related to egg density·m^2 bottom area (Kynard et al., 2010; Fig. 4). In the artificial spawning stream, the maximum number of larvae produced was 8000–16,000 (about 425–851 larvae·m^2 of bottom area. Annual production of larvae in the artificial stream (156−16,002) was significantly related to egg density with the greatest survival from egg to larva (31.98%) from an estimated density of 1,938 eggs·m^2. Larval habitat has not been studied in the wild but artificial stream studies found CR SNS larvae foraged on the open bottom on drift and did not use cover (Kynard and Horgan, 2002a).

External Biology and Functional Morphology.

A. General characteristics

The ultrastructure of SNS sperm is different from the sympatric AS (DiLauro et al., 1999). This suggests a deep evolutionary separation of the two species, which has been corroborated by recent phylogenetic analyses (see Phylogenetics Section).

Characteristics that distinguish SNS from AS are a wide mouth (width exceeds 62% (range, 63−81%) of interorbital width, pre-anal shields usually a single row, usually no preanal shields between the row of lateral scutes and anal base, a black peritoneum, four long barbels and a short blunt snout in adults (Dadswell et al., 1984). However, the overall morphology of SNS, particularly of the snout and head shape generally (Hilton and Bemis, 1999; 2012), is highly variable. Mouth width is the most reliable character for distinguishing between SNS and AS within the size range of SNS.

Data on the skeletal anatomy of SNS have been included in several recent comparative and descriptive studies (e.g., Hilton and Bemis, 1999; Hilton, 2002, 2004, 2005), including a recently completed monographic osteological study, including aspects of skeletal development, by Hilton

(2011). Scutes are sharp and close together in larvae and juveniles. Typically, scutes become blunt and more widely spaced in adults, and in some large individuals, the scutes (particularly on the lateral and ventral rows) become almost completely resorbed (Hilton and Bemis, 1999).

Body color of ELS follows: embryo (dark brown to black); free embryo (dark brown to black); larva, initially a light-gray body and black tail − the black-tail phenotype of Kynard and Horgan (2002a), becoming all dark gray body with increasing age. The possible adaptive significance of the black-tail phenotype is discussed in Kynard and Horgan (2002a and in ten papers by the first author on ontogenetic behaviour of sturgeon ELS. Body color details on juvenile and adult life stages are in Snyder (1988): juvenile (dorsal−dark blackish, ventral−light gray) with black blotches scattered over the entire body (which gradually disappear with age) paired fins edged in white, scutes paler color than body on some fish; and adult (dorsal− blackish-bronze with metallic green-blue sometimes, ventral−light gray to cream), scutes often paler color than body, paired fins edged in white. The black body blotches on juveniles, which are shared by juvenile LS, may be for camouflage, but their adaptive significance has not been studied.

Development of scutes and the small bony plates embedded in the skin has not been studied but in CR SNS, their development is much greater in downstream segment juveniles and adults (with access to salt water in the estuary) compared to upstream segment juveniles and adults living in fresh water (Kynard, B., unpbl. data). The difference in scute development between the two population segments may reflect the ability of downstream segment SNS to forage in the estuary where a higher concentration of minerals is available for scute development.

B. Swimming speed

Swimming of adults and juveniles has been observed during development of upstream and downstream fish passage facilities and the species has a moderate swimming ability and does not jump to pass upstream or downstream in passage facilities. Kynard et al. (2012f) found CR SNS males moved upstream for 38 m in a side-baffle ladder swimming at 1.7 $BL \cdot s^{-1}$ (prolonged swimming mode) to pass the fastest velocity of about 1.2 $m \cdot s^{-1}$ in baffle slots. Life history also supports this laboratory result because CR SNS adults must swim upstream through two 5 rkm long rapids (Kynard et al., 2012a, e). Pre-spawning adults must swim upstream through several rapids in the SJohnR (Litvak, M., pers. comm.).

Swimming speed of SJohnR juveniles was recently studied in the laboratory (Kieffer et al., 2009). Critical swimming speeds (mean + SEM) for juveniles ranging in total length from 14 to 18 cm was 34.4. + 1.7 $cm \cdot s^{-1}$ or 2.18 + 0.09 $BL \cdot s^{-1}$ (a similar result to the swimming speed during fish passage of adults found by Kynard et al., 2012f). Swimming challenges revealed SNS were relatively poor swimmers (compared to salmonids) and did not significantly modify their swimming behaviour in response to increasing velocities. When exposed to higher velocity challenges, juveniles spent more time in contact with the substrate, exhibiting "skimming" behaviour (Kieffer et al., 2009).

Internal Biology

A. General characteristics

Feeding frequency and meal size affects growth of juveniles (Gibertson and Litvak, 2003), and growth rate of SNS varies inversely with latitude. Fish from northerly populations grow more slowly than fish from southern populations (Dadswell et al., 1984; Moser et al., 2000). This relationship is thought to be related to a temperature effect rather than to different population traits

(Dadswell et al., 1984). Hardy and Litvak (2004) reared SNS and AS at different temperatures (13, 15, 18, 21 ^{o}C) after hatch and measured yolk utilization rate and efficiency, maximum standard length, survival, and development of escape response. Newly hatched AS were smaller in size, more efficient at utilizing yolk (incorporating yolk to body tissue) and reached developmental stages sooner than SNS reared at the same temperatures (13 and 15 ^{o}C). Within each species, decreasing temperature delayed yolk absorption, escape initiation, time to reach maximum size, and time to 100% mortality.

However, yolk utilization efficiencies and the size of larvae were independent of rearing temperature for both species. These results suggest that even as temperature drives metabolic processes to speed up development, both species are still extremely efficient at transferring yolk energy to body tissues. The lower efficiencies experienced by larval SNS may reflect difference in yolk quality between the two species or AS may have a higher conversion efficiency. The ability of both species to develop successfully and efficiently under a wide range in temperatures may provide a competitive advantage over more stenothermic species and may contribute to their persistence through evolutionary time.

Shortnose Sturgeon jump out of the water throughout the species range. Adults were observed to periodically swim vertically from the bottom to break the water surface in a 7-m deep flume (Kynard et al., 2005). Vertical swimming (and jumping?) may be related to regulation of air in the swim bladder in this physostomous fish.

B. Tolerances

Ziegeweid et al. (2008a) recently examined both the lethal thermal maxima and acclimation temperature for SNS YOY (0.6−35 g). They found that the lethal maxima was 34.8 and 36.1^{o}C for

fish acclimated to water at 19.5 and 24.1°C, respectively. This suggests the potential for high summer temperatures experienced by southern populations to be lethal to YOY and the possibility that YOY search for temperature refugia.

Jarvis et al. (2001) examined the effect of salinity on growth of SJohnR SNS. Juveniles (mean weight, 273 g) were grown at four salinities (0, 5, 10, and 20 ppt) for 10 wk at 18°C. Weight gain and Feed Conversion Rate (FCR) decreased with increasing salinity. Fish reared at 0 ppt showed significantly more weight gain and greater FCR than fish raised at all other salinities. Fish reared at 20 ppt salinity exhibited the poorest growth. Ziegweid et al. (2008b) recently examined the salinity tolerance of SavR YOY and found the 50% lethal maxima for salinity after 48 h exposure was 14−21 ppt. They also found an interaction between salinity tolerance and temperature that resulted in decreased survival with an increase in temperature and salinity. However, this effect was ameliorated with an increase in body size for same age fish. Juveniles do not develop tolerance to salinity levels found in estuaries until about 1 yr of age, a similar finding as Jenkins et al. (1993).

Collins et al. (2000) suggested deterioration in water quality is affecting nursery production of southern juvenile SNS and that low DO levels in nurseries may be a recruitment bottleneck. Mid-Atlantic and southern populations evolved in rivers with both high summer river temperatures and low DO concentrations (although linkage of temperature and DO may not be direct), but climate warming will result in increased summer temperatures (and possibly, lower DO levels). This change is not presently as big a problem for SNS in northern rivers. Secor and Nicklitschek (2001) suggested that absence or reduced populations of both SNS and AS in some rivers was a result of low DO levels. He also hypothesized that the increased abundance of SNS in the HudR was due to a return to normoxia. Because cessation of SNS harvest occurred concurrently with

improvement of DO levels, determination of causality for the increase in SNS is not possible.

Aspects of internal chemistry of SNS are being studied in DelR SNS to gather baseline data on annual and season variability for adults (Matsche et al., 2012b). One factor of hematology (PVC) varied seasonally and reflected sexual maturity. Seasonal and gender variation was found for some factors: higher levels of sodium, chloride, and proteins in fall and higher levels of calcium and total protein in mature females compared to immature females or males. Glucose was also higher in females than in males, suggesting different energetic requirements between the sexes. The results on energetic requirements of the sexes are supported by field studies on wintering CR females and males, where females lose a greater percent of their somatic body weight than males (Kieffer and Kynard, 2012b).

C. Exercise physiology

There are a few studies on exercise of SNS (Kieffer et al., 2001; Baker et al., 2002, 2005). These researchers used forced activity to examine the physiological responses to exercise of AS and SNS. Oxygen consumption and ammonia excretion in both species and a variety of physiological parameters in both muscle (e.g. lactate, glycogen, pyruvate, glucose, and phosphocreatine concentrations) and blood (e.g. osmolality, lactate, total protein, ion concentration and cortisol) were recorded on juveniles following exhaustive exercise. Oxygen consumption and ammonia excretion rates increased approximately twofold following exhaustive exercise. Post-exercise oxygen consumption rates decreased to control levels within 30 min in both sturgeon species, but post-exercise ammonia excretion rates remained high in AS throughout the 4 h experiment. Resting muscle energy metabolite levels were similar to those of other fish species, but the levels decreased only slightly following the exercise period and recovery occurred within an hour. Under

resting conditions, muscle lactate levels were low (<1 mumol·g^{-1}), but they increased to approximately 6 mumol·g^{-1} after exercise, returning to control levels within 6 h. Unlike similarly stressed teleost fish, such as Rainbow Trout (Salmo gairdneri), plasma lactate levels did not increase substantially and returned to resting levels within 2 h. Plasma osmolality was not significantly affected by exercise in both species. Taken together, these results suggest that SNS and AS do not exhibit the physiological responses to exhaustive exercise typical of other fish species. They may possess behavioural or endocrinological mechanisms that differ from those of other fishes and that lead to a reduced ability to respond physiologically to exhaustive exercise.

Parasites and Disease

Dadswell et al. (1984) presented a checklist of parasites found on SNS in 1) the SJohnR, 2) the upstream segment in freshwater of the CR, and 3) a coastal migrant captured at Woods Hole, MA. Both internal and external parasites were found, but the authors concluded that none likely had a major harmful effect on adults. It should be noted, however, that should a deleterious parasite or pathogen outbreak occur, its spread could be hastened by the interbasin movements now recognized in this species, particularly in the GOM and southern parts of the range.

No diseases have been found to be associated with wild SNS and many years of rearing eggs to adults at low densities at the Conte AFRC found only one major disease: bacteria (Columnaris) that occurs on captive fish gills following high river discharge during the summer−fall. Cultured eggs (and eggs naturally spawned in the artificial stream; Kynard et al., 2012c) were commonly infected with Saprolegnia fungus. Finally, cultured SNS sometime develop “bloat syndrome”, especially when temperatures decrease in fall, which occurs in other sturgeon species (Kynard, B., unpbl. data). The latter problem has not been reported in wild populations, but wild individuals

with the problem either quickly recover or probably die.

Genetics

A. Chromosome number

The Acipenseriformes are all polyploid, with large numbers of chromosomes (Kim et al., 2005). Shortnose Sturgeon is a hexaploid species, with the greatest number of chromosomes of any species of Aciperseriformes, i.e., 2n = 372 ± 6 (Fontana et al., 2008). Adaptive significance of polyploidy is poorly understood, but may be related to retaining genetic diversity during inbreeding (suggesting during evolution of Acipenseriformes, small inbreeding populations may have been common).

B. Population genetics

Range-wide genetic analyses using mitochondrial DNA (mDNA) from SNS adults in 11 rivers or estuaries (SJohnR, KenR, AndroR, CR, HudR, DelR, Chesapeake Bay, CapeFR, CoopR, SavR, and OgeeR found differences between all except for DelR versus Chesapeake Bay (Grunwald et al., 2002). The authors made several conclusions: 1) no discrete populations are likely within the Chesapeake Bay as adults found there were all migrants from the DelR, 2) significant haplotype differences exist even between KenR and AndroR populations, showing genetic differences between populations within the same large KenR estuary system, 3) gene flow estimates among populations were generally higher than expected at the north and south extremes of the range, and 4) the high percent of unique haplotypes in the northern populations suggest SNS survived glaciations in a northern refugia. The data also suggested a five-region genetic grouping of populations. Additional mitochondrial DNA examination of SNS sampled from 14 rivers found discrete populations in nine rivers: SJohnR, KenR, AndroR, CR, HudR, DelR, Winyay Bay,

1716 GPeeR, SavR, and AltR (Wirgin et al., 2009; Fig. 6). The samples of SNS from the CoopR and
1717 Lake Marion (upstream from dams) were similar, supporting the hypothesis that CoopR, SantR,
1718 and Lake Marion SNS are segments of one population that has been disrupted by damming, like
1719 the CR SNS population. The SavR and OgeeR samples were similar, supporting fish tracking
1720 information that the OgeeR is a river used for foraging and refuge for SNS from other rivers.
1721 The most recent range-wide study of the patterns of SNS genetic variation was performed
1722 using polysomic nuclear DNA (King et al., 2014; Fig. 6). Intra-specific examination of the nuclear
1723 genome revealed the presence of considerable allelic diversity and differentiation that reflects
1724 actions of various evolutionary processes. Phylogeographically, these research findings suggest the
1725 presence of similar levels of genetic diversity and variation among the collections punctuated with
1726 a series of genetic discontinuities of varying 'depth' across the range that could indicate
1727 demographic independence, regional adaptive significance, or vicariant geographic events.
1728 Populations sampled within these regional groupings exhibited shallow but statistically significant
1729 differentiation. All patterns of population relatedness were consistent with the observations of
1730 Kynard (1997) that populations at both ends of the range are more dispersive than those in the
1731 middle. The increased rates of gene flow in the northern and southern collections appear to reflect
1732 the greater geographic proximity of rivers in these areas relative to those in the northeast rivers
1733 (CR, HudR, and DelR).
1734 King et al. (2014) identified two major ("deep") zones of genetic discontinuity in the nDNA:
1735 1) separation of the GOM and northeast collections, and 2) separation of the northeast and southern
1736 populations (Fig. 6). These zones of genetic discontinuity demarcated three major groups of SNS
1737 collections: GOM, northeast, and Southern. Moreover, narrower ("shallow") zones of genetic
1738 discontinuity between the CR and HudR and between the HudR and an apparent DelR–

1739 Chesapeake Bay metapopulation further delineated a total of three distinct evolutionary lineages
1740 within the northeastern and mid-Atlantic (Chesapeake Bay) regions: CR, HudR, and the DelR–
1741 Chesapeake Bay proper. This brings to five (5) the number of demographically and evolutionary
1742 distinct lineages identified within the USA portion of the SNS range based on nDNA allele
1743 phenotypes. A recently obtained sampling of 22 pre-spawning MR males had patterns of nDNA
1744 variation that suggest this group is genetically different from adults in other GOM rivers.
1745 Additional sampling is needed before conclusions can be reached about genetic differentiation of
1746 MR SNS from the GOM metapopulation.
1747 In addition to the five demographically discrete and evolutionarily significant lineages
1748 identified for SNS within the USA, three metapopulations and many other distinct individual river
1749 populations are delineated that may be considered distinct management–recovery units for future
1750 recovery planning purposes. The three metapopulations are the: 1) major Maine rivers (i.e.,
1751 PenobR, KenR, and AndR), 2) DelR and Chesapeake Bay, and 3) the entire southern grouping
1752 (GPeeDR, SantR-CoopR, EdisR, SavR, OgeeR, and AltR, and Lake Marion; Fig. 6). Population
1753 biology theory predicts that smaller isolated populations are at greater risk of demographic
1754 extinction than similar populations linked through dispersal in a metapopulation (Hanski and
1755 Gilpin, 1997). Likewise, genetic isolation of very small populations can in theory lead to decreased
1756 genetic diversity and inbreeding in small isolated populations, and thus creates adverse
1757 consequences for fitness (Frankham, 2005). Given recent tagging and tracking data showing SNS
1758 migrate to adjacent rivers to a greater extent than previously believed (Smith et al., 2002;
1759 Fernandes, 2008; Dionne, 2010; Zydlewski et al., 2011; Wippelhauser et al., 2015) concomitant
1760 with the identification of at least three metapopulations within the range, suggests that species risk
1761 should take into account such demographic benefits. On the flip side, greater connectivity among

populations introduces new threats, such as those that might impair migratory corridors or an increase potential for spread of disease. That said, there is still some modest evidence of divergence in multilocus phenotypes among river systems within metapopulations. Hence, it could be argued that the basic unit for management and conservation (recovery planning) of SNS is still the individual (local) population (or deme), as was suggested by the Recovery Team in 1998.

King et al. (2014) also performed a quantitative comparison of the metrics describing genetic differentiation for both mtDNA and nDNA (Fig. 7). Examination of the multidimensional scaling scatter plots depicting the structure contained within the pair-wise mtDNA Φ_{ST}(Wirgin et al., 2009) and nDNA Φ_{PT} distance matrices suggested the presence of three major groupings representing the GOM, northeastern, and southern populations (Fig. 6). Moreover, similar patterns of differentiation were observed in the genomes among the northeastern populations as the CR, HudR, and DelR–Chesapeake Bay populations appear differentiated in both genomes. The respective scatter plots also suggest the presence of at least three regional metapopulations; Maine rivers (i.e., PenobR, KenR, and AndR), DelR and Chesapeake Bay proper, and Southern (CapFR-Winyah Bay rivers, SantR-CoopR, EdisR, SavR, OgeeR, AltR, and Lake Marion). However, a difference in patterns between the two metrics is visible as the maternally-inherited mtDNA pair-wise distances (Φ_{ST}; range 0 – 0.614, mean = 0.308) were on average an order of magnitude greater than that observed with the nDNA distance (Φ_{PT}; range 0 – 0.307, mean 0.155). Regardless of this distinction, the degree of congruence for the detectable genetic differentiation was statistically comparable. A Mantel analysis comparing the pair-wise Φ_{PT} and Φ_{ST} distance matrices for 14 Atlantic Coast collections of SNS identified a strong statistical relationship (correlation coefficient $r = 0.84$, $P < 0.0001$) between the variation detected in these genomes.

Microsatellite DNA markers have been shown to underestimate genetic divergence between

populations due to the high mutation rate that can generate hyper-polymorphism in repetitive regions of DNA (Hedrick, 1999; Balloux et al., 2000). The polyploid SNS genome presents an increased potential for allele size homoplasy. Moreover, because of the presence of polysomic banding patterns, the alleles were scored as phenotypes. As a result of these limitations, some 'penalty' will be realized as observed phenotypic diversity is likely to be an underestimation of the differentiation that exists among populations; particularly for those that have experienced extended reproductive isolation. Although quantitative variation and molecular variation are at times correlated, adaptive population structuring often far exceeds neutral population structuring, even for populations diverging over contemporary time (Koskinen et al., 2002; Stockwell et al., 2003; Kinnison et al., 2008). Therefore, the estimates of allelic differentiation detected at neutral loci by King et al. (2014) should be considered an underestimation of the divergence present.

The large disparity in magnitude between Φ_{ST} and Φ_{PT} values could be due to the distance metrics used in this comparison assessing the influence of fundamentally different evolutionary processes (Fig. 7). Φ_{ST} quantifies sequence divergence (mutational steps) between haplotypes as well as measures frequency differences. Φ_{PT} treats all nDNA allelic phenotypes as equally differentiated (i.e., distance = 1.0) regardless of the number of alleles present or differences in fragment size, and assesses the variance distribution based on allele frequencies alone. Differences between allele frequencies are assumed to be due to genetic drift. Thus, uniformly larger Φ_{ST} values indicate that a portion of the observed differentiation is due to evolutionary processes other than gene drift.

Alternatively, the observation of across the board greater mtDNA haplotype differentiation relative to nuclear DNA differentiation (Φ_{PT}) may indicate the existence of fundamentally different reproductive behaviours between female and male SNS. Differential vagility could lead to less

gender-mediated gene flow between adjacent populations and greater differentiation. If true, this would indicate a trend toward reduced philopatry (i.e., sex-biased dispersal) in males throughout the range. Indeed, limited life history information supports this idea, i.e., only ripe females from the DelR apparently migrated to the PotR to spawn (Kynard et al., 2009).

The presence of demographically distinct and evolutionary significant lineages delineated by zones of genetic discontinuity is consistent with the findings of researchers assessing behavioural patterns in ELS of SNS populations. Parker and Kynard (2005, 2014) found that during common garden experiments (testing behavioural responses of many populations to common environmental factors), ELS dispersal behaviour was locally adapted to each river. These researchers demonstrated differences in the innate dispersal patterns in ELS from the CR and SavR and suggested young SNS have different behavioural adaptations (particularly, for dispersal style) to unique features of their watershed. Similar adaptive differences have been inferred for behaviour of ELS of other sturgeon species like LS (Wolf and Menominee rivers; Kynard, B. unpbl. data) and between sub-species of AS: HudR AS and Suwannee River GS (Kynard and Horgan, 2002a; Kynard and Parker, 2004).

Fisheries and Impacts

Although incidental capture of SNS by recreational anglers (i.e., hook-and-line fishers) occurs in many rivers (Dadswell et al., 1984; Collins, M., unpbl. data; Kynard, B., unpbl. data), no surveys have been done to determine the rarity of captures. The effects of various levels of fishing on three populations of SNS (SJohnR, HudR, and GPeeDR) showed the impact of life history differences on yield per recruit and the harvest strategy needed to preserve populations (Boreman, et al., 1984). The model suggested a low harvest level of F0.1 leaves adequate spawning stock in northern or southern populations. However, the authors noted that even a harvest level of F0.1

1832 should be approached cautiously because other sources of mortality are not quantified.
1833 Additionally, Boreman (1997) found AS, WS, SNS, and Paddlefish (Polyodon spathula) were
1834 more susceptible to fishing mortality than three other fish species commonly harvested along the
1835 Atlantic Coast. The susceptibility of sturgeons and Paddlefish to overharvest was due to their
1836 characteristic life histories.
1837 Population modeling of SNS assumes spawning occurs each year by all mature females;
1838 however, spawning totally fails for all females during some years in the CR, and likely, in other
1839 northern (and southern) populations (Kieffer and Kynard, 2012a; Peterson, D., unpbl. data). Until
1840 the frequency of spawning failure is documented and can be predicted in SNS populations,
1841 modeling recruitment and the effect of harvest on any population will be inaccurate.
1842 In the 1940s, fishermen targeted upstream segment CR SNS and likely harvested hundreds of
1843 adults or a significant proportion of the population segment (Kynard, B., unpbl. data).
1844 Additionally, throughout the range, SNS aggregate annually in the same reaches of a river, so their
1845 predictable movements make them susceptible to harvest throughout the range. Once the
1846 aggregation sites are known, fish can be easily targeted with gill or trammel nets. Thus, managers
1847 should be alert to this possibility in all rivers.
1848 Bycatch of SNS in the commercial shrimp trawl fishery off southern states has been
1849 documented (Collins, M., unpbl. data) and may have occurred in near-shore waters. The use of
1850 turtle excluders (TEDs) may reduce the potential for sturgeon bycatch, but more data on bycatch of
1851 SNS by commercial trawling is needed.
1852 Some directed poaching of SNS with gill nets has been documented (Collins, M., unpbl.
1853 data; Cooke, D. SC Dep. Nat. Resour., Bonneau, unpbl. data), but the impact from this activity is
1854 unknown on any population. Poaching may be limited due to the potentially severe federal

1855 punishments specified for poaching of SNS as an endangered species.

1856 The primary unintended fishery impact on SNS in rivers is the commercial gillnet fisheries
1857 for American Shad (Alosa sapidissima). These fisheries, which are regulated by each state, occur
1858 annually in the lower reaches of many coastal rivers within the range of SNS. In all rivers
1859 throughout the range of SNS, the spring SNS spawning migration coincides with the spawning
1860 migration of American Shad. Coincidentally, the gillnet mesh size commonly used by commercial
1861 fishermen (usually 12.7 cm stretch mesh), is also efficient at capturing adult SNS (Dadswell et al.,
1862 1984). Collins et al. (1996, 2000) suggested bycatch mortality is one of the two major deleterious
1863 factors preventing recovery of southern SNS. In SC and GA, Collins et al. (1996) found that the
1864 CPUE of SNS in American Shad gill nets was $0.003-0.137 \cdot h^{-1}$. Further, 16% of the captured SNS
1865 died immediately and another 20% were injured. However, recent evidence on bycatch mortality
1866 of SNS was < 8% in the commercial American Shad fishery in the AltR (Bahn et al., 2012).
1867 Perhaps, handling SNS in the bycatch has improved since the 1990s study by Collins et al. (1996).
1868 In addition, capture and handling of pre-spawning SNS by American Shad fisherman (or
1869 researchers) can result in an important non-lethal impact (fall-back), cessation of migration, and
1870 migration failure (Moser and Ross, 1995).

1871 For southern rivers, which have a lower abundance of SNS than in northern rivers, fishery
1872 impacts may be an important impediment to recovery. A partial solution may be to eliminate
1873 anchored gill nets and allow only drift (tended) gill nets in the American Shad fishery. Although
1874 drift nets may capture more adult SNS if fished in the channel, SNS could be released more
1875 quickly than using anchored nets, thus avoiding mortality of SNS. This would allow the
1876 continuation of the fishery and minimize mortality to SNS, but would not avoid SNS aborting their
1877 spawning migration after capture and release (Moser and Ross, 1995). The historical drift gill net

fishery for CR American Shad was estimated to capture only a few SNS annually (likely <tens of fish; Savoy, T., Connecticut Dep. Environ. Prot., Old Lyme, unpbl. data); however, this estimate was not scientifically verified.

Major Anthropogenic Impacts

Major impacts on SNS throughout the range are damming, impingement and entrainment at hydropower plants, alteration of physical river habitat by channelization and dredging, hypoxia, and pollution. This list of direct impacts has not changed since the status of SNS was evaluated by Dadswell et al. (1984) and Kynard (1997). In recent years, there are also possible direct impacts to southern populations from unintentional introduction of foreign sturgeon species and from rice farming (Jaeger et al., 2013), to northern populations from the advent of coastal (tidal) hydropower development, and to all coastal rivers from climate warming.

A. Damming and river regulation

Damming blocks the upstream spawning migration of some SNS populations (review, Kynard 1997), and in some rivers, significantly restricts the extent of freshwater larval and juvenile rearing habitat, i.e., Pinopolis Dam on the CoopR (Cooke and Leach, 2004). Holyoke Dam on the CR blocks three types of SNS migrations: upstream non-spawning, pre-spawning staging, and spawning. A similar situation likely exists in the SanR−CoopR complex (Kynard, 1997; Collins et al., 2003; Cooke and Leach, 2004; Finney et al., 2006; Kynard et al., 2012a).

Some SNS adults on spawning migrations blocked by a dam spawn in the dam's tailrace (Cooke and Leach, 2004; Duncan et al., 2004; Kynard et. al., 2012b) even though ELS will not begin life at the upstream spawning site evolved by natural selection. For populations where ELS

1901 stages have evolved a long dispersal requiring a long freshwater reach, spawning farther down-
1902 stream below a dam that is near the estuary likely results in death of the dispersing life stages,
1903 which lack salinity tolerance (Jenkins et al., 1993; Parker and Kynard, 2005).

1904 Evolution of spawning site selection involves a site with suitable habitat for gametes during
1905 spawning, eggs during incubation, and free embryos, if they rear at the spawning site. However,
1906 evolution of site selection also incorporates ultimate factors important for survival of larva, which
1907 is the main dispersing early life stage in SNS populations and where most mortality occurs during
1908 life history (Gross et al., 2002; Kynard and Horgan, 2002a; Kynard et al., 2012c). Thus, damming
1909 that greatly shortens the freshwater reach compared to the length of the natural freshwater dispersal
1910 reach that ELS have evolved to use may greatly affect survival and recruitment of young SNS.
1911 Further, in the CR, predation intensity on SNS larvae and early-juveniles is likely much more
1912 intense the closer the larval-early juvenile rearing reach is to the estuary because abundant
1913 diadromous fish predators occupy the lower river (Merriman and Thorpe, 1976). Connecticut River
1914 SNS spawn upstream of two long rapids at about rkm 200, and few diadromous predators forage so
1915 far upstream, so predator avoidance may also be a factor in the evolution of spawning reach
1916 selection (Kynard, pers. obs.).

1917 Upstream passage of SNS at dams can be provided by several methods: a fish elevator, a
1918 side-baffle ladder or ladder of similar design, or a semi-natural bypass (Kynard, 1998; Kynard,
1919 2008; Kynard et al., 2012f). However, the cost difference among these choices is vast. Design
1920 criteria are not available for a semi-natural bypass, but much is known about SNS behaviour and
1921 swimming ability relative to structure and current speed that can contribute to a design. The side-
1922 baffle ladder developed by Kynard et al. (2011a, 2012f) for sturgeons and other migratory fish
1923 with a moderate swimming ability resembles a natural river chute and passed adult SNS, LS, and

juvenile Green Sturgeon = GRS (A. medirostris), and many riverine fish species. Further, the fish lift at Holyoke, which was not designed or is operated to pass SNS, has passed a few SNS over many years. Kynard (1998, 2008) discusses important factors for passing SNS in fish lifts, including the Holyoke fish lift.

Although downstream passage structures or other means of protecting SNS from injury during downstream passage at dams is poorly understood and a prototype was installed in 2015 at Holyoke Dam, it has not been evaluated. Kynard and Horgan (2002c) found louvers were a superior guidance structure compared to bar racks for juvenile SNS; Amaral et al. (2002) also tested bar racks for guiding SNS. Kynard et al. (2005; unpbl. data) tested SNS in large flumes to develop a bypass system composed of guidance louvers and a submerged orifice bypass for downstream migrant sturgeons attempting to pass dams. Recently, a research plan for developing fish passage for SNS, AS, and GS was prepared for NMFS (Kynard and Pugh, 2011b). This plan could assist development of fish passage for sturgeons in the South.

The effects of river regulation on SNS range-wide are poorly studied. The impacts of river regulation on CR SNS involve determining spawning success by forcing females to leave their natural spawning reach and move to a hydroelectric station's tailrace, where turbine flows can change quickly making suitable bottom velocity, unsuitable for spawning (Kieffer and Kynard, 2012a). Also, ELS spawned in a tailrace likely have poor survival due to variable turbine operation, which can create flows that sweep ELS downstream or bury them with sediment (Kieffer, M. and Kynard, B. unpbl. data). How peaking operations by hydroelectric dams affect summer foraging and energetics of SNS has not been studied.

B. Impingement and entrainment

For upstream segment adult CR SNS that migrate downstream past Holyoke Dam, some migrants (22 of 49 tagged adults) entered a turbine at the Hadley Falls Generating Station at the dam and 100% of these adults were killed (Kynard et al., 2012a). Survival of yr-1 upstream segment CR SNS migrating past Holyoke Dam should be less than the passage mortality of 11.8−13.7% for similar size Atlantic Salmon (Salmo salar) smolts estimated at these turbines (Steir and Kynard, 1986). Data on yr-1 SNS passage mortality is needed, but all studies suggest most yr-1 SNS should survive passage.

Impingement and entrainment of SNS also exists in the Santee-Cooper system (Cooke and Leach, 2003; Kynard et al., 2012a), although there is controversy over this situation (Collins et al., 2003). As restoration of SNS proceeds in southern rivers, upstream and downstream passage will be required at many dams (Cooke et al., 2002; Cooke and Leach, 2003, 2004; Kynard and Pugh, 2011; Kynard et al., 2012a).

Few SNS adults are impinged on trash racks of power plants, but YOY and juveniles have been impinged. In its long history of operation, the Yankee Nuclear Power Plant on the CR has impinged only one adult (Kynard, B., unpbl. data) even though many adults and juveniles as young as yr 1+ are likely present. Two juveniles were impinged at the Mt. Tom Coal Fired Generating Plant in MA (Kieffer, M., unpbl. data). At power plants in the HudR, adults and large juveniles are not impinged, but larvae and juveniles as young as YOY are regularly impinged (Carlson and Simpson, 1987; Dovel et al., 1992) with 163 YOY impinged on intake screens at the Albany Steam Generating Station during 1 yr (Shortnose Sturgeon Status Review Team, 2010). Early-migrant larval SNS will not likely be entrained and not detected if they enter water withdrawal systems, even those with screens. Even if these larvae are impinged on a screen, their bodies will not likely remain intact in the fast intake velocities and early-larvae can pass undetected through a 3/8” clear

opening (Kynard, B., unpbl. data).

C. Channelization, substrate alteration, and dredging

Channelization of lower river reaches used by SNS has been extensive in southern rivers (Collins, M., unpbl. data), but northern rivers have also been extensively modified (Haefner, 1967; Kinnison, M., unpbl. data; Kynard, B., unpbl. data). In northern river systems, modifications were commonly made in the form of shoreline filling and reinforcement for mills and other industry or in the form of in-river structures like rock booms and weirs for lumber operations or shipping. In some systems, these activities contributed to significant alteration of the historical substrate, with increased sedimentation and deposition of sand and other materials. Extensive lumber transport and milling in some northern rivers contributed directly to extensive deposition of wood debris, sawdust and bark in lower reaches of rivers and estuaries of the GOM. Indeed, these soft sediments are known to extend to depths of >3 m in some parts of the PenobR frequented by SNS (Metcalf and Eddy, 1994) and a similar situation exists in the St. Marys River, GA (Rogers et al., 1994).

Dredging in the lower reaches of rivers that includes the freshwater: saltwater zone likely has a great impact on reducing recruitment of SNS in most rivers. The freshwater: saltwater zone is where YOY and juveniles rear throughout the species' range (Hall et al., 1991; Collins et al., 2002; Rogers and Weber, 1994a, b, 1995; Bain, 1997; Brundage and O'Herron, 2009; Kynard et al., 2012a). This impact was demonstrated many years ago when dredging in the shipping turning basin in the SavR destroyed juvenile habitat (Collins et al., 2002; Collins, M., unpbl. data). Dredging occurs in the lower reach of almost all rivers in the USA with SNS, yet even though life history information indicates yearling and older juveniles rear in this reach of river, this impact has received little directed study and management agencies have traditionally deferred to a lack of

information. As recently as 2008, dredging was federally permitted immediately adjacent to the summer aggregation and overwintering habitat of SNS in the PenobR. Although adult monitoring was required in coordination with dredging activities, juveniles were not monitored because no study indicated they were present (Kinnison, M., unpbl. data). Destruction of juvenile rearing habitat in river estuaries by dredging or other alterations has not been adequately addressed in any river within the species range. When expansion of the Panama Canal is completed in a few years, there will be great pressure to alter and deepen ports in the South to enable the larger container ships to enter southern ports. Additionally, in the lower reaches of some southern rivers, there is increased pumping of groundwater, which can result in saline water intruding into previously freshwater reaches and a decrease in juvenile SNS habitat (Jaeger et al., 2013). Modification of the freshwater: saltwater zone from any cause has the potential to deleteriously impact SNS because yearlings rear there.

D. Water quality alteration

The extreme case where DO level is too low to support fish life is rare but can occur where pulp mills and other polluting facilities contaminate rivers. This situation may have resulted in the low DO levels <3 $mg \cdot l^{-1}$ in river reaches used by SNS and AS in summer and led to unsuitable habitat for SNS in the Satilla and St. Marys rivers (Rogers and Weber, 1994a, b). Recent tracking of SNS in the OgeeR found SNS in a summer refuge reach led to the development of methods to assess the relationships between habitat use and water quality (Farrae et al., unpbl. data). The methods in this study have applicability to SNS in all rivers.

Hypoxic conditions are commonly documented in the lower PenobR, due to the significant sediment load and biological oxygen demand (BOD) prior to water quality improvements in the

2016 last decades of the 20th century. The current presence of SNS in the PenobR may be in part due to
2017 the supportive effects of population connections to neighboring systems that allowed SNS to
2018 obtain refuge from hypoxia and recolonize following mortality events (Fernandes, 2008; Fernandes
2019 et al., 2010).

2020 Shortnose Sturgeon in GOM and northeastern rivers (KenR, PenobR, MR, CR, and HudR)
2021 survived the pollution peak of the Industrial Revolution in North America showing the species can
2022 survive high levels of chemical pollution, although the deleterious effects on populations were
2023 likely severe. Although 25 yr ago tumors (Kynard, B., unpbl. data) and fin fungus (Dovel et al.,
2024 1992) were commonly observed on SNS from the CR and HudR, respectively, these problems are
2025 not observed today on adults. Both populations survived more than 100 yr of the worst chemical
2026 and biological pollution present in any Atlantic coast river. Data on the specific effects of chemical
2027 pollution on SNS are rare due to the lack of study. Even today, SNS in some northeastern rivers
2028 may carry significant body contaminant burdens. Alteration of hormone levels and sex in DelR
2029 SNS by discarded hormones from humans was suggested by the study of Matsche et al. (2012a) on
2030 DelR SNS. This situation needs to be monitored carefully because of the potential for hormones to
2031 alter the sex and demography of an entire SNS population.

2032

2033 **Other Stochastic Natural Impacts**

2034 Weather-related phenomena can determine the success of various life history activities, many that
2035 seem related to bioenergetics. For example, river conditions in summer-fall likely affects foraging
2036 efficiency of CR SNS which may determine the energetic condition of wintering pre-spawning
2037 adults and determine whether females will have the energy to make a pre-spawning migration in
2038 spring after wintering (Kieffer and Kynard, 2012a). Also, the amount of rainfall that occurs and the

timing of rain events likely determine the passage success of CR adults that attempt to swim upstream through two rapids to their upstream concentration reach for foraging or pre-spawning staging (Kynard et al., 2012a). Weather also determines river discharge during the spawning period. If the river is too high or too low, bottom velocities acceptable to pre-spawning females may not occur when the photoperiod windows are open for spawning and spawning will fail.

Although SNS in any river have adapted to flooding, flooding in the CR can affect spawning success, survival of ELS, and habitat use. The greatest impact may be on ELS, e.g., attached eggs and free embryos hiding under rocks that can be buried by sand or displaced from spawning habitat at the spawning reach during high flow events. Drifting eggs−free embryos likely are injured or killed from hitting the bottom or after drifting into saline water (Kynard and Horgan, 2002a; Parker and Kynard, 2005; Kieffer and Kynard, 2012a). Floods may also affect foraging and survival of larvae. Also, high river discharge in summer (and in winter) may have caused an energetic crisis for pre-spawning CR adults and caused spawning migration failure the following spring (Kieffer and Kynard, 2012a).

Stranding of SNS can occur just downstream of dams in relation to natural decrease in river flow and hydroelectric dam operations. Stranding of CR SNS occurred frequently just below Holyoke Dam when natural spillage water over the dam was quickly stopped to create additional water for generating electricity (Kynard et al., 2012b). In situations where SNS occur just downstream of a dam, spill ramping rates should gradually decrease to give SNS sufficient time to find a water flow exit. Stranding of SNS has not been observed in open-river rapids, likely because water levels go down gradually, allowing fish to escape.

The dietary reliance of SNS in some rivers on bivalve mollusks makes them potentially susceptible to bioaccumulation of toxins from toxic algae blooms or other pollutants in the

2062 mollusks. In July 2009, 14 dead SNS and AS were found floating or on beaches near the mouth of
2063 the KenR−AndR system, which was coincidental with an intense red tide bloom. Post-mortem
2064 tissue analyses suggest that consumption of contaminated shellfish was responsible for the SNS
2065 mortalities. It is difficult to ascertain the relative threat that such blooms present to SNS; however,
2066 it is likely that in the KenR-AndR system, far more fish were killed or sub-lethally impaired than
2067 the 14 bodies that were recovered.
2068
2069 ## Emerging Impacts, Threats, Risks
2070 ### A. Chemical pollution
2071 In the chemical environment, the impact of endocrine disrupting chemicals = EDCs on SNS is not
2072 known, but could have a major effect on reproduction. Adult SNS collected from the DelR had
2073 concentrations of polychlorinated dibenzo-p-dioxins (PCDDs), polychlorinated dibenzofurans
2074 (PCDFs), polychlorinated biphenyls (PCBs), dichlorodiphenyldichloroethylene (DDE), aluminum,
2075 cadmium, and copper in gonad and liver tissue above adverse effect concentrations reported for
2076 other fish species (Environ. Res. and Consult., Inc., 2002). PCDDs, PCDFs, PCBs, DDE, and
2077 cadmium have been identified as EDCs, and there is evidence that the adverse effects of these
2078 chemicals may be exacerbated when they occur in combination (Monosson, 1997). On the positive
2079 side, water quality in GOM, northeastern, and mid-Atlantic rivers has improved as a result
2080 improved federal and state regulations.
2081
2082 ### B. Climate change
2083 Climate change could have a great impact on SNS if predictions of river warming are realized and
2084 rainfall patterns drastically change. Climate change could greatly affect the success of life history
2085 of SNS throughout the species range. Movements, spawning, and energetics have evolved to adapt

SNS populations within a range of river discharges, water temperatures, water quality, and salinities. We already know that temperature can affect SNS larval dispersal, so a long-term increase in river temperature during larval dispersal could result in non-adaptive larval dispersal and put selective pressure on spawning timing and larval dispersal to adapt to changed conditions. Thus, climate change and warming of rivers may change river discharge, temperature, and chemistry creating a mis-match between population adaptations and the rapidly changing environment. Temperature increases are predicted throughout rivers in the northeast, like the DelR (Miara et al. 2013). Further, sea level rise associated with climate change could result in salinity intrusion into nursery rivers that historically have been fresh water (Kreeger et al., 2010). In rivers where the freshwater:saltwater rearing zone of young sturgeons has been destroyed by construction of harbors for large ships, the effect of salt water intrusion may be a long-term positive factor for SNS if it moves their rearing zone upstream away from the boat harbor. Increased rainfall during the photoperiod controlled spawning window could be a problem for spawning of SNS if it creates greater bottom velocities that are outside the velocity preferenda of females. Effects of climatic change on SNS are extensively discussed by the Shortnose Sturgeon Status Review Team (2010).

Impacts could also be severe near the southern margin of the range where SNS are already experiencing summer conditions (high temperature, low DO) that are, in some cases, near the species tolerance limits in summer, especially for YOY (Jenkins et al., 1993). If recruitment failure occurs repeatedly in southern rivers, SNS eliminated and range of the species contracted by nearly 50% compared to the historical range (unless there is range expansion into new northern rivers, an unknown possibility). The genetic differences between northern and southern populations (King et al., 2014) suggest southern populations may be pre-adapted to warm conditions, an adaptation that

could protect southern populations under a warming environment. However, studies are needed to test this hypothesis.

C. Interactions with other protected species

Recovery of marine mammals has increased the abundance of one of the few natural predators on adult SNS – marine mammals. Grey Seal (Halichoerus grypus) have been observed preying on adult SNS (Fernandes, 2008). Bite marks on MR SNS are also likely from seals (Kieffer, M., unpbl. data), indicating this impact is on all GOM SNS populations. This situation presents a challenging management dilemma that places two federally protected species in conflict with one another. Predation by seals and sea lions on endangered salmon and WS in the Pacific Northwest provides some insight into the complexities of this challenge (Fraker and Mate, 1999).

Less direct challenges are posed by the limitations placed on sturgeon research and management as a result of protections afforded other threatened or endangered species. For example, in the PenobR system, protections afforded endangered Atlantic Salmon limits the scope for some basic research activities, such as netting for juvenile sturgeons, that could provide information on population status (Kinnison, M., unpbl. data). Conflicts among endangered and threatened species are likely to become an increasing challenge as more species are listed with overlapping ranges.

D. Development of tidal power

Tidal power is currently being evaluated to determine its potential to produce electricity in the Bay of Fundy and along the northeast coast of the USA. The specific location for development is in the Minas Basin, where tides are among the highest on Earth. Turbines used for generating tidal power will likely impact the coastal migrations of many species (Dadswell and Rulifson, 1994). While

SNS have not been recorded in the Minas Basin, the expansion of tidal power to other regions in the GOM may directly interfere with SNS movements, and also, injure or kill SNS. Similar concerns exist for tidal power development in the northeast outside of the GOM.

Population Recovery Actions

Shortnose Sturgeon was originally listed as an endangered species by the USFWS on 11 March 1967, under the Endangered Species Preservation Act (ESA). The species continued to meet the listing criteria as "endangered" under subsequent definitions specified in the 1969 ESA. NMFS assumed jurisdiction for SNS from the USFWS under a 1970 government reorganization plan. The ESA was enacted in 1973 and all species that were listed as endangered species threatened with extinction in the 1969 ESA were deemed endangered species under the ESA. SNS currently remains listed as an endangered species throughout its range along the East Coast of the United States. Although the original listing notice did not cite reasons for listing the species, a 1973 Resource Publication stated that SNS were "in peril ... gone in most of the rivers of its former range [but] probably not as yet extinct" (USDI, 1973). Pollution and overfishing, including bycatch in the American Shad fishery, were listed as principal reasons for the decline.

The status of SNS was last examined in 1987; however, the status review report was never finalized by NMFS. Subsequently in 1994, the status of SNS in the AndrosR and KenR rivers was assessed in response to a petition to de-list the population. Delisting was not warranted based on a number of factors by NMFS. A SNS Recovery Plan was published in 1998 (NMFS, 1998) and guidelines for using the species published in 2000 (Moser et al., 2000). In 2007, NMFS initiated a status review to determine if the ESA listing classification was accurate. The status review was completed in 2010 (Shortnose Sturgeon Status Review Team, 2010). The report includes a

summary of published literature and other currently available scientific information regarding the biology and status of the SNS, as well as an assessment of existing regulatory mechanisms and current conservation and research efforts that may yield protection.

Recovery is the process by which species listed under the ESA, along with their ecosystems, are restored and their future is safeguarded to a point that protections under the ESA are no longer needed. Both NMFS and USFWS are charged by the ESA to develop recovery plans for listed species. Recovery Plans usually include descriptions of management actions, objective and measurable criteria to determine when a species can be removed from the ESA, and estimates of time and cost to carry out measures required for recovery.

The 1998 Recovery Plan and the 2010 status review concluded the conservation of each of the 19 populations was essential. This conclusion was based on the concept that substantial reproductive isolation of SNS existed between rivers and river systems. Since the 1998 Recovery Plan, the status of spawning in several rivers and genetic studies have clarified the status of some populations and identified evolutionary distinct lineages. Using genetic analysis coupled with tagging data, we can better identify genetic structure within the SNS taxon. Recent genetic studies found there are five distinct evolutionary lineages of SNS in the USA: CR, HudR + three meta-populations: GOM, DelR-mid-Atlantic, and southern. Additionally, distinct river populations have been identified. Adding the distinct SJohnR population in Canada makes six distinct evolutionary lineages in the SNS range.

Assessing threats is critical to realizing actions required for recovery of a listed species. The causes of the decline of the species, threats to the species, and the source of those threats are the cornerstone to identifying elements essential to the recovery of the species. Factors affecting recovery of SNS and their habitat were identified in the Recovery Plan and are summarized in

2178 Table 1. After threats are identified, conservation efforts to reduce or remove threats should be
2179 identified along with partners and stakeholders. Partners to assist in the recovery of SNS identified
2180 in the Recovery Plan included Federal agencies (NMFS, USFWS, USGS, FERC, FHWA, NRC,
2181 EPA, USACE) and individual state agencies.

2182 The Recovery Strategy for SNS is to recover all discrete population segments to levels of
2183 abundance at which they no longer require protection under the ESA. Each segment can become
2184 considered for downlisting when it reaches a minimum population size that: 1) is large enough to
2185 prevent extinction, and 2) will make the loss of genetic diversity unlikely. Specific parameters and
2186 a minimum population size for each population were not specified in the Recovery Plan (NMFS,
2187 1998); instead, this was determined to be a top priority as a Recovery Task (Table 2). Then, in
2188 order to preserve the minimum population size, essential habitat was to be identified and
2189 maintained, while monitoring and minimizing mortality.

2190 Shortnose Sturgeon is currently considered by NMFS to have a moderate level of threat with
2191 a high recovery potential. A high potential for recovery indicates threats are mostly understood and
2192 management actions to reduce threats are identified in the Recovery Plan. However, the
2193 relationship between threats to the species and tasks to remedy those threats are not clear in the
2194 Plan. Recovery tasks should directly address the means by which to reduce threats to the species
2195 and its habitat.

2196 The 1998 SNS Recovery Plan is outdated and requires an update. A new Recovery Plan
2197 should continue to focus on riverine populations, but recognize the importance of metapopulation
2198 processes (demographic and genetic) as well as the critical corridor habitats that support them.
2199 This may mean some adjustment to how such a plan identifies threats and tasks to reduce those
2200 risks. Conservation actions should be at both the regional level and at the local source of stressors

level. Further, a new Recovery Plan should seek to identify more partners and include stakeholders in order to best conserve the species, specifically expertise on restoring rivers.

Recently, NMFS published a helpful report containing protocols for capturing, handling, tagging, etc. for SNS and other protected sturgeon species (Kahn and Mohead, 2010). This expanded the earlier protocol of Moser et al. (2000) and provides extensive guidance to researchers. Additionally, there is long-term data on handling, immobilizing, and telemetry tagging SNS in Kieffer and Kynard (2012d).

Research Needs

Many research needs were identified in the Recovery Plan (NMFS, 1998); they are updated and summarized in Table 2. Much has been accomplished in terms of meeting various recovery objectives; however, no research objective is complete. A sampling protocol has been finalized (Kahn and Mohead, 2010) and tissue samples are being collected and archived for genetic analysis making range-wide genetic assessments possible (Walsh et al., 2001; Grunwald et al., 2002; Quattro et al., 2002; Wirgin et al., 2005, 2009; King et al., 2014).

The list of necessary life history research is lengthy and is particularly needed on southern populations, which is likely the major emphasis on the species in the 21st Century. Comprehensive information on distribution, population dynamics, larval and juvenile movement and behaviour (particularly, YOY and yr-1 juveniles), and factors leading to reproductive success are needed in order to assess the demic status of SNS. New and reliable estimates of population size and recruitment would help determine status of riverine populations. As noted previously, a method to accurately age juveniles and adults throughout the range is greatly needed. Telemetry will allow a better understanding of inter-river and intra-riverine movements and connections. Range-wide

genetic or genomic assessments would help further determine which differences across the geographic range are likely adaptive a result of vicariance and drift. Ontogenetic dispersal patterns are different between CR and SavR populations, and information on other populations could be used to characterize discrete populations. This behaviour should be studied in many populations to provide the best life history information to correspond with genetic differentiation of river populations. Research and testing to refine sturgeon-passage around locks and dams for both upstream and downstream movements would improve access to restricted spawning or foraging habitats. Diet studies to better define preferred prey across life stages are needed to specify foraging reaches; as well as aggregation reaches. Potential nursery reaches and a characterization of that habitat is a priority as young life stages are not well-studied in rivers. The thermal niche for SNS needs to be better understood and this is important for wintering fish as well as summering fish. Laboratory studies on yr-3 SNS, yr-2 LS, yr 1-2 GS, yr-1 GRS, yr-2 AS, and yr-1 WS found that wintering juveniles were attracted by warm temperatures (Kynard and Henyey, 1999; Parker et al., 2012a; Kynard et al., 2014b). These results suggest heated power plant effluent discharged into mid-Atlantic, northeastern, and GOM rivers or estuaries near a natural wintering area could attract SNS (and other species of sturgeons) disrupting natural seasonal patterns of feeding, growth, gonad maturation, and reproduction. These results, plus the known effect of increased temperature on larval dispersal (Parker, 2007), and the wide latitudinal range of the species, suggest SNS would make an excellent subject to study the effect of increased temperature from climate change on ELS behaviour and life history.

A better understanding of the potential effects from new and ongoing anthropogenic actions would assist agencies in mitigating and eliminating adverse impacts. Information defining essential elements and characterizing spawning and foraging habitats would assist in not only identifying

these important areas, but also defining environmental parameters to assist agencies in ensuring these habitats are not indirectly impacted by anthropogenic actions occurring nearby. Potential effects of contaminants and nutrient enrichment from human activity on sturgeon are not understood; maximum load levels that consider the benthic SNS should be examined and identified. Impacts of dredging and disposal related to abundance and recovery of SNS prey items has not been investigated. Dredging removes sediments, disturbs the benthos, and re-suspends sediments and contaminants. Subsequent disposal places large amount of sediment on the benthos that can suffocate benthic macrofauna. In the process, benthic prey composition and abundance can modify the benthos to such a degree that sturgeon prey may no longer be able to inhabit the area.

Without developing the knowledge base to develop fish passage for SNS at dams in southeastern rivers, many populations will not be able to recover. Thus, there is a critical need for research information on all aspects of sturgeon passage.

Current Prognosis for Species

Under the federal and state protection given SNS during the past 40 yr, abundance of northern populations has increased or at least remained stable. New information suggests other positive trends for the species. The discovery of adults, a spawning migration, and presence of spawning habitat in the PotR (Kynard et al., 2009) suggests the absence of SNS in Chesapeake Bay Rivers, may change with natural colonization of rivers by DelR adults or with an increase in remnant populations. Mid-Atlantic SNS are needed to provide a genetic connection between northern and southern populations. The PotR and other rivers in VA need to be carefully monitored and surveyed for SNS.

Most southern populations are impacted by damming. However, there is no upstream or downstream passage for migrant SNS at any dam in the South. A solution needs to be found for this problem or impacted populations will not recover. The same goes for CR SNS, where upstream migrations have been blocked since 1849, creating a dysfunctional life history and killing many downstream migrants that pass through turbines at the dam since the late-1950's (Kynard et al., 2012a, e). Planned removals of dams in the PenobR may reconnect fish to historic spawning and ELS rearing habitats, potentially enabling SNS to colonize, and perhaps, spawn there.

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Table 1. Factors affecting recovery of Shortnose sturgeons (SNS) and their habitats (NMFS, 1989).

Threat	Effect to SNS	Effect to Habitat
Commercial & Recreational Fishing	Mortality, abandonment or interruption of spawning migration, injury	
Bridge Construction & Demolition	Interrupts normal migratory movements , turbidity, internal damage or mortality from noise	Disturbs areas of concentration, sedimentation of spawning areas, burial of eggs
Contaminants & Point Source Discharge	Lesions, growth retardation, reproductive impairment, reduced fitness, reduced survival of larvae and juveniles, behaviour alteration, deformation, reduced egg production and survival	Environmental contamination and bioaccumulation
Dams	Mortality, reduced viability of eggs, limits population growth	Restricts access to habitat, fragments populations, alters river flow, turbidity,
Dissolved Oxygen	Mortality, interferes with movement	Decreases available habitat in water column
Dredging	Mortality, injury, disrupts spawning migrations,	Destroys benthic foraging areas, sedimentation of spawning areas,
Cooling Water Intakes & Power Plants	Impingement, entrainment	Excavation, dewatering and dredging increases turbidity and destroys habitat and prey resources. Reduced water quality
Reservoir Operation	Thermal effects, miscued migration	Alters natural river flow rate and volume, hypoxic or anoxic water conditions
Thermal Refuges	Limit population survival, juvenile mortality	Loss of habitat
Introductions & Transfers	Increased predation, reduction of prey, genetic, competition for food and habitat, disease	Competition for available habitat and prey

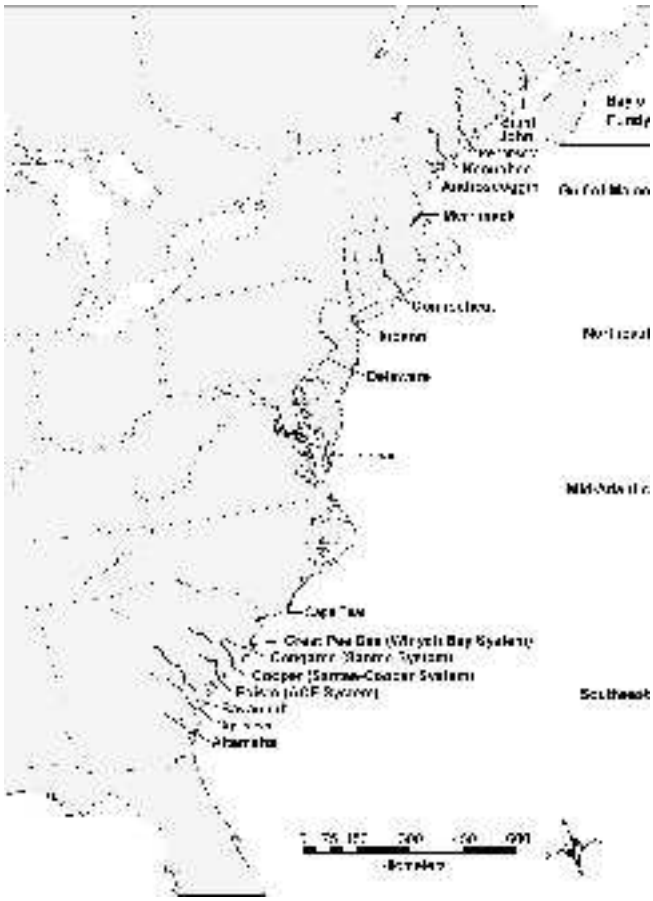
Table 2. Summary of tasks and research activities by objective from SNS Recovery Plan (NMFS, 1998).

Task	**Associated Research**
Establish Listing Criteria	
Determine the size of SNS population segments for listing and evaluate trends in recruitment	
Conduct a range-wide genetic assessment of SNS	Collect tissue samples, conduct appropriate genetic analysis.
Develop a standardized sampling protocol and determine minimum sampling required to assess presence of SNS	Collaboration with researchers, compilation of ongoing methodology and data collection.
Determine abundance, age structure, and recruitment of SNS	Survey and conduct population assessment in each river.
Determine endangered and threatened population size thresholds	Data collection at population-level, evaluate population dynamics to determine population stability. Conduct a status review for each population segment.
Determine minimum habitat for riverine populations	Using population size and carrying capacity, identify size of habitat to accommodate all stages of the life cycle.
lish criteria to identify essential habitat	Conduct research (mark recapture, telemetry, survey sampling, etc.) indicating SNS seasonal distribution. Identify habitat requirements, establish criteria to establish essential habitat, utilize GIS, incorporate field observations and physiological requirements and map concentration areas to characterize critical habitat. Identify and, if prudent, designate critical habitat for SNS population segments.
Determine maximum allowable mortality	Assess mortality factors and define take limits for each

for each riverine population	population.
Protect SNS populations and habitats	
Insure agency compliance with the ESA & establish Section 6 agreements	Encourage agencies to fulfill responsibilities, insure actions do not jeopardize, provide support for research. Establish Best Management Practices.
Reduce bycatch & minimize the effects of incidental capture. Increase enforcement	Identify seasonal or areal limits on problem fisheries. Recommend handling procedures. Assess SNS mortality from incidental capture and document characteristics of fisheries that impact SNS (gear types, fishing season and location, fishing effort, etc.). Conduct research to determine sub-lethal effects of incidental capture and provide guidelines to minimize bycatch mortality and sub lethal effects (i.e. reduce soak times, reduce handling time, gear modification, etc.). Develop genetic markers to identify illegal products.
Determine if critical habitat designation is prudent	Identify critical habitat, conduct field research to document usage and identify changes in habitat use.
Mitigate/eliminate impact of adverse anthropogenic actions	Insure fish passage devices allow adequate passage of SNS and do not alter migration or spawning behaviour. Conduct research to assess the direct and indirect effects of blasting dredging, and in river disposal on all life stages of SNS. Compare impacts of various dredging, blasting, and disposal techniques and equipment on SNS and their habitat to minimize the detrimental effects of these activities. Conduct research to assess SNS mortality from entrainment and impingement and maximize efforts to obtain scientific information from dead fish. Study effects of point and non-point source pollution and reduce harmful levels.
Assess degree of contamination in SNS tissue, food and habitats	Analyze tissue, food items, and sediment/water samples from SNS habitat to assess the degree of contaminant loading and determine effects on growth, survival and reproduction. Collect continuous recordings of dissolved oxygen in SNS habitat to identify the extent and duration of hypoxic events. Conduct studies to determine tolerance. Identify introduced species and stock transfers and determine the extent and results of parasitism,

	disease, competition for resources, and direct mortality resulting from introduced species and stock transfers.
Formulate a public education program to increase awareness	Print and distribute articles, pamphlets and posters. Display cultured SNS in aquariums and zoos. Update media on recovery actions by publishing news articles. Work with schools.
Coordinate federal, state and private efforts to implement recovery tasks	Appoint Recovery Coordinator and establish regional Recovery Implementation Teams. Establish communication network. Seek funding. Complete periodic updates to Recovery Plan.
Rehabilitate habitats and population segments	
Restore access to habitats	In each river, identify natural migration patterns of each life stage and any barriers to movement between habitats. Devise methods to pass SNS above/below existing barriers.
Restore access to spawning habitats and conditions	Examine the relationships between river discharge level, substrate type, and SNS spawning success. Investigate the relationship between spawning substrate characteristics and SNS reproductive success. Conduct field experiments to evaluate the ability of natural river discharge to remove sediment and debris from spawning substrate; and evaluate the acceptability of artificial substrate to spawning females.
Restore foraging habitat	Investigate satisfactory methods for examining diet. Determine diet range-wide, foraging ecology, and growth, for each life stage. In populations with poor growth, examine foraging habitat characteristics and conduct experimental manipulations, if appropriate, to restore habitat.
Reduce deleterious contaminant concentrations	Identify contaminants and reduce loading.
Resolve project conflicts	Establish consistent operating policies that allow agencies to meet mission goals while protecting fish and habitat.
Develop a breeding and stocking protocol	Duplicate natural conditions, select donor stocks carefully.
Reintroduction into rivers where extirpated	Use standardized protocol to determine need. Determine minimum population size below which restoration may be considered. Monitor survival, movement patterns, distribution, foraging and reproduction. Evaluate success.

Assess need for augmentation & adhere to strict conditions	Determine cause for low abundance. Correct poor habitat conditions. Conservation stocking only **short-term** to supplement a population faced with extirpation.



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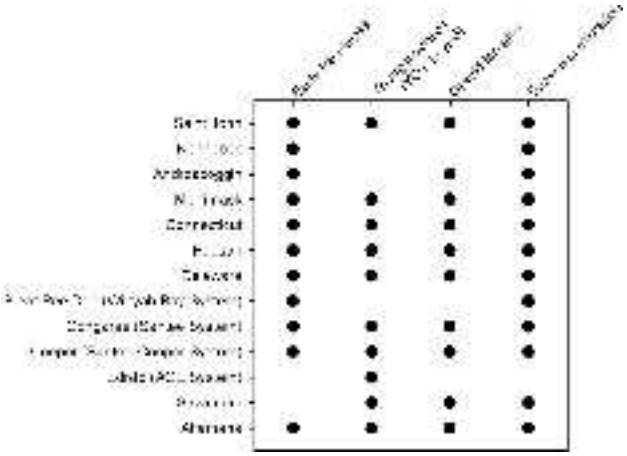

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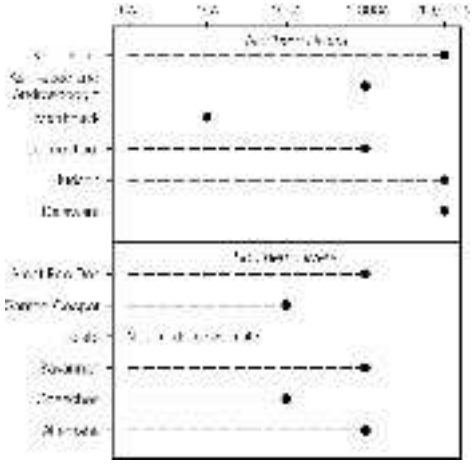

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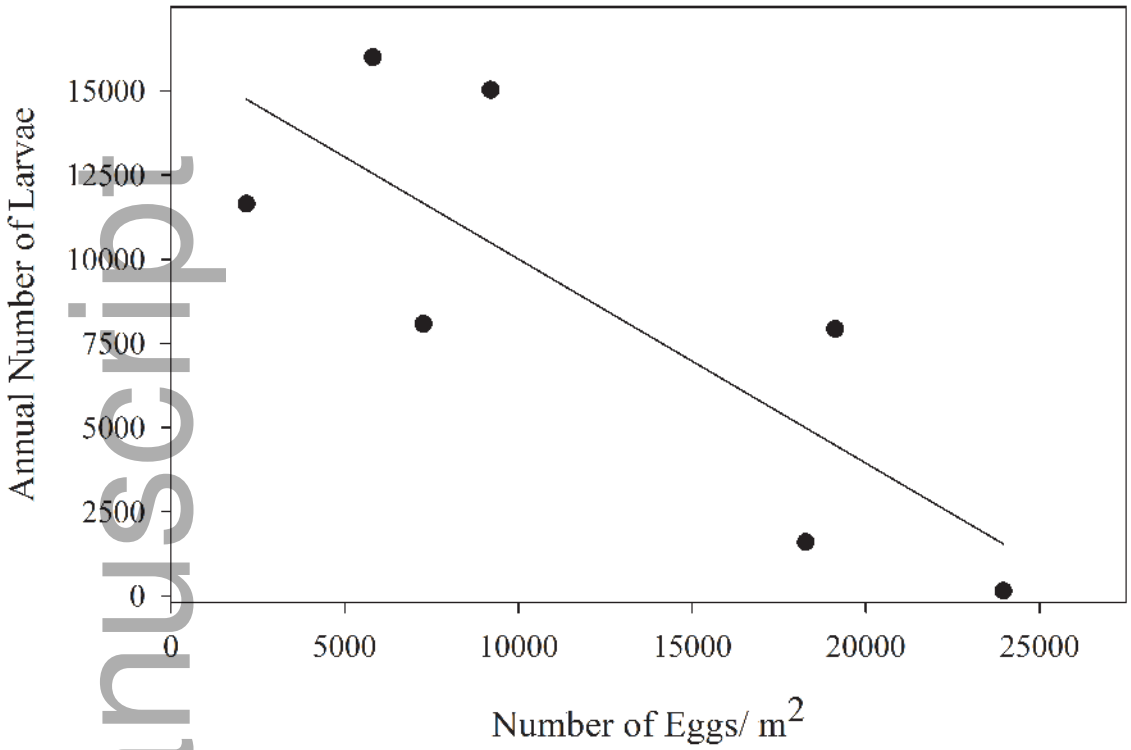

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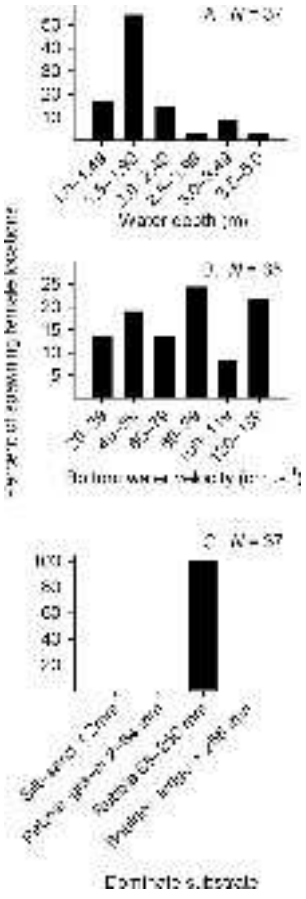

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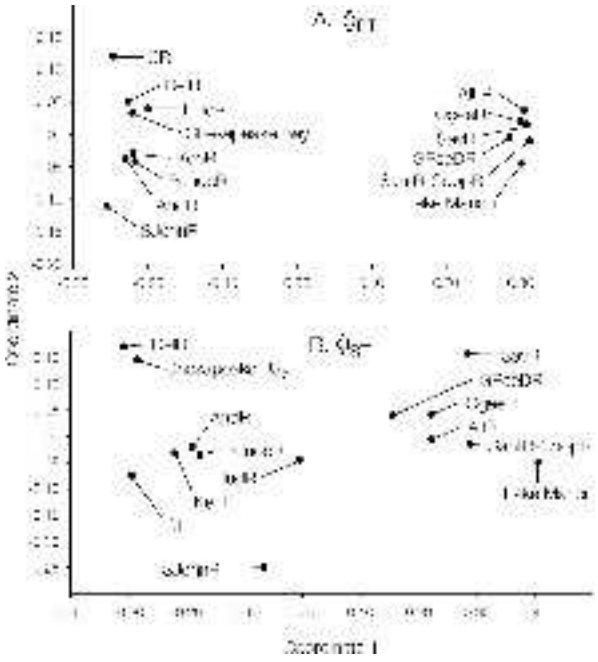

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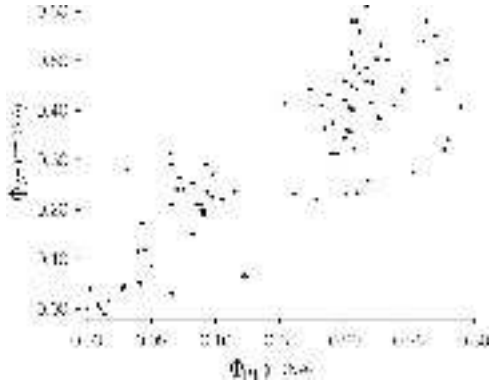

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